ENVIRONMENTAL AND STOMATAL PHYSIOLOGY OF *NOTHOFAGUS* SEEDLINGS

A thesis

submitted in partial fulfilment

of the requirements for the Degree

of

Doctor of Philosophy in

Plant Physiology

in the

University of Canterbury

by

Paul R. van Gardingen

University of Canterbury

1987

CONTENTS.

LIST OF FIGURES.

FIGURE PAGE

LIST OF TABLES

TABLE PAGE

ABSTRACT.

The Maruia Valley on the West Coast of the South Island of New Zealand is a region with *Nothofagus* forest dominated by mixtures of *N. fusca* and *N. menziesii*. The Station Creek area was selected for environmental and gas exchange measurements with the two species.

The mean daily temperature and vapour pressure deficit (VPD) variation was found to be up to two times higher on an open logged site than under both closed canopy and a small canopy gap. The light flux under closed canopy was 5% of that measured in the open. During summer the light flux under the canopy gap was up to 25% of that in the open.

Gas exchange was measured using a LI-COR LI-6000 portable photosynthesis system. An improved set of formulae were developed for this system and have been implemented in a computer programme for the IBM PC and compatibles.

Gas exchange measurements at Station Creek were used to determine the maximum rates of photosynthesis (A_{max}) and stomatal conductance (g_{max}) as well as the sensitivity of these estimates to VPD. The rates of gas exchange were higher in *N. menziesii* than *N. fusca*. No significant difference was found between species for the estimates of stomatal and photosynthetic sensitivity. In addition there was no difference between foliage growing in the open, under a canopy gap, or under closed canopy.

Gas exchange measurements of saplings growing in a nursery at Rangiora on the east coast of the South Island gave similar results during early summer. As the season progressed, the rates were lower at Rangiora due to moderate water stress.

It is suggested that *Nothofagus* seedlings have a wide ecological tolerance, which is in part due to the generalized stomatal response to VPD. This can explain how *Nothofagus* is capable of regenerating under a wide range of environmental conditions. Under extreme environments seedling growth is reduced and regeneration will succeed only in the absence of rapidly growing competing species.

1. INTRODUCTION.

1.1 GENERAL.

The four species of *Nothofagus* native to New Zealand are a major component of more than 60 percent of New Zealand's remaining indigenous forest. 'Pure' beech forest covers approximately 46 percent of the 6.25 million ha of indigenous forest (Wardle 1984). Mixtures of beech with softwoods and broad-leaved hardwoods cover a further 22 percent (Wardle 1984).

Much of the remaining beech forests grow in geologically unstable areas and are zoned as protection forests. These forests are managed to control soil erosion, water quality, and catchment yield (Morris 1970). Areas of forest have also been reserved for ecological, scientific and scenic reasons, with the potential for recreation and tourism only starting to be realized. The areas of indigenous forest zoned for production represent 25 percent of the total resource (Wardle 1983) of which 13 percent is still virgin forest (1974 figures).

When the New Zealand Forest Service was set up in 1920 it began an extensive survey of the indigenous forests (Kirkland 1974). Leonard Cockayne was commissioned to study the New Zealand beech forests and produced two monographs, one covering the ecology and taxonomy of the beech (Cockayne 1926), and the other aspects of forest management (Cockayne 1928).

Since Cockayne's work in the 1920's there has been little research conducted on beech forests. Much of the published work covers beech management and was reviewed by Gleason (1982). The early ecological work was mostly of a descriptive nature and relied heavily on comparison with similar species in the northern hemisphere. The Forest Service proposals (N.Z. Forest Service 1971) to utilize large areas of South Island beech forest prompted new research into ecological and management aspects of these forests. Wardle (1984) reviewed the ecology of the New Zealand species of *Nothofagus*. The plant associations in which beech is found have been well described, but little information is available on the processes controlling the establishment and growth of *Nothofagus* species. Several other authors have noted the lack of this information (Cockayne 1926, Kirkland 1974, Wardle 1983, 1984)

1.2 The GENUS *Nothofagus*.

The genus *Nothofagus*, often referred to as 'Southern beech' belongs to the Fagaceae, a family of woody trees and shrubs which also includes *Quercus* (Oak), *Castanea* (chestnuts), and *Fagus* (Northern beech). *Nothofagus* and *Fagus* together form the sub-family Fagoideae. All species of *Fagus* are deciduous whilst most of the 34 species of *Nothofagus* currently recognized are evergreen (Wardle 1984). The four species of *Nothofagus* native to New Zealand fall into two groups. The larger

group includes *N. fusca* (Hook f.) Oerst (Red beech), *N. truncata* (Col.) Ckn. (Hard beech), *N. solandri* var. *solandri* (Hook f.) Oerst (Black beech), and *N. solandri* var. *cliffortioides* (Hook f.) Poole (Mountain beech). These species maintain most of their foliage for only one season, with maximum leaf fall coinciding with bud burst in spring and have been called winter-green by some workers (e.g. Benecke and Evans 1986). *N. menziesii* (Hook. f.) Oerst (Silver beech) is more closely related to Australian and South American species of *Nothofagus* than the other three native species and maintains its foliage for up to three seasons.

1.3 GENERAL ECOLOGY.

'Pure' beech forest in New Zealand has a relatively simple structure and is not as floristically complex as other indigenous forests types. The dense understorey which characterizes the subtropical rain-forest is not present, and consists mainly of beech seedlings and saplings. The ecological preferences of the four species were reviewed by Wardle (1984). *N. solandri* var. *cliffortioides* grows mainly at higher altitudes or on infertile, poorly drained, or dry sites. *N. menziesii* also grows at high altitude, usually in regions of high rainfall and is less tolerant of infertile or poorly drained sites. *N. menziesii* is also found at lower altitudes in association with *N. fusca*. *N. fusca* is restricted to fertile well drained sites. It is the most site demanding species of *Nothofagus* in New Zealand and grows mostly on lower and mid slopes. *N. truncata* and *N. solandri* var. *solandri* are limited to low altitude sites. They are more tolerant of infertile soils and drought prone regions than *N. fusca*. *N. truncata* is intolerant of low temperatures and tends to grow in the northern regions of the country with a southern limit at 42° 30' S (Wardle 1984).

The generalized life history of New Zealand beech can be split into four phases.

1. Establishment:- which is a prerequisite for a plant to occupy any site.
2. Suppression:- characterized by extremely slow growth rates of seedlings growing under an intact forest canopy .
3. Release:- characterized by rapid growth and intense competition by seedlings growing under a canopy gap or on a open site.
4. Canopy:- eventually formed after the rapid growth and self-thinning during the release phase.

1.4 PHYSIOLOGY.

The limited work that has been conducted on the physiology of New Zealand's *Nothofagus* species relates mainly to adult trees. The freezing resistance of *N. solandri* and *N. fusca* twigs was compared with other native trees and *Nothofagus* species from Australia and South America by Sakai and Wardle (1978). In a related study, Wardle and Campbell (1976) investigated winter dormancy of

N. solandri var. *cliffortioides* seedlings near timber line in the southern alps. Jane and Green (1983) used pressure volume techniques to study drought resistance of several native woody species including *N. menziesii*. They found that *N. menziesii* had adaptations for drought resistance but did not compare it with other species of *Nothofagus*.

The water and carbon relations of adult *N. truncata* growing in a mature uneven-aged stand were investigated by Benecke and Evans (1986). Gas exchange measurements were combined with biomass data to model annual carbon balance and water use for the stand. The empirical models developed in their study describe stomatal and photosynthetic responses to important environmental parameters. Respiration rates were calculated using temperature curves to estimate the respiratory temperature coefficient (Q_{10}) (Benecke 1985). The photosynthetic model was based on responses to temperature, light and atmospheric vapour pressure deficit (VPD) and the model for stomatal conductance responses to light and VPD. The stand model used measurements of specific leaf area to scale net carbon gain and water use allowing for differences between sun and shade foliage and seasonal effects.

The study found that leaves showed considerable physiological adaptation to the light regime in which they grew. Sun leaves had maximum photosynthetic rates (A_{max}) of between 5 and 10 μmol m^{-2} s^{-1} (on a projected area basis). A_{max} of shade foliage was significantly less and light saturation occurred at lower intensities. Stomatal and photosynthetic sensitivity to VPD depended on leaf age with newly expanded foliage having the strongest response. The response declined as the season progressed and was lower in shade than in sun foliage. A stronger response to VPD was observed during a moist summer compared to the previous year's drought.

The gas exchange of *N. solandri* var. *cliffortioides* was investigated at a range of altitudes on the southern alps (Benecke *et al.* 1976, Benecke and Havranek 1980a, Benecke and Nordmeyer 1982). These studies showed similar rates of photosynthesis as the study by Benecke and Evans (1986) with *N. truncata*. The physiological differences between sun and shade foliage observed in *N. truncata* by Benecke and Evans were also found in *N. solandri* var. *cliffortioides* by Benecke and Nordmeyer (1982). Similar results have been reported for *Fagus sylvatica* (Schulze 1970) and with seedlings of Tasmanian and South American species of *Nothofagus* (Read 1985, Read and Hill 1985) .

Read and Hill (1985) compared photosynthetic characteristics in seedlings of five species of *Nothofagus* from Australia and Chile. They found that seedlings grown under shade had lower light compensation points, respiratory rates and A_{max} values than seedlings grown under direct sunlight. The specific leaf area and chlorophyll content per unit area were higher in shaded seedlings. These results

are typical for a comparison between sun and shade foliage (Bjorkman 1981, Boardman 1977).

The physiological characteristics of suppressed and released *Nothofagus* seedlings have not been investigated for any of the New Zealand species. Plants growing under a canopy need to be adapted to the highly modified environment which is characterized by low light, high humidity and water availability. Suppressed seedlings might be expected to have adaptations to maximize carbon gain whilst seedlings growing under a large canopy gap would have adaptations to limit water loss. When a group of suppressed seedlings are released by the opening of a canopy gap, the stomatal physiology of the plants could change to adapt to the modified environment. Detailed measurements are required of the important environmental factors together with the physiological responses of plants to these factors.

1.5 SEEDLING ESTABLISHMENT.

Nothofagus seedlings can establish under a wide range of environmental conditions, with all the native species capable of germinating under a closed canopy. They also are able to establish on more open sites and bare mineral soil in the absence of rapidly growing 'weed' species. Environmental factors influencing seedling establishment and subsequent growth have been reported in several studies (Cockayne 1926, Franklin 1974, Franklin and Beveridge 1975, Kirkland 1974, Manson 1974, Wardle 1983, 1984). However there have been few attempts to quantify their effects on regeneration.

The environment under a forest canopy is highly modified by the presence of the forest. The sub-canopy environment is buffered with less extreme conditions than experienced above the canopy or on large open sites, for example daily temperature variation is lower under a canopy than on open sites. Soil surfaces in the open may experience lethal temperatures during summer, and severe frosts with associated frost heave during winter. The higher maximum temperatures observed on open sites cause increased evaporative demand and may increase plant water loss.

Nothofagus seedlings are highly susceptible to desiccation, particularly during the first year's growth (Wardle 1984). Survival during this phase depends on adequate water availability. The potential water usage by the plant is determined by the atmospheric evaporative demand. A measure of the evaporative demand is the atmospheric vapour pressure deficit (VPD). The higher temperatures on open sites result in higher vapour pressure deficits than under a closed canopy and may limit plant growth on a open site.

The growth and survival of seedlings under a fully closed canopy is limited by light availability. Seedling mortality of *N. solandri* var. *cliffortioides* and *N. fusca*

has been found to be lower under partial shade than either full sunlight or dense shade (Wardle 1970, June and Ogden 1975). These studies found that the optimal light treatment was about 35 percent of full sunlight.

On sites which experience full sunlight, seedling establishment can be limited by rapidly growing 'weed' species. In several areas fern species principally *Blechnum discolor* (Crown fern), *Pteridium esculentum* (Bracken) and *Histiopteris incisa* (Water fern) prevent seedling establishment by forming a dense ground cover (Franklin and Beveridge 1975, Gleason 1982, Wardle 1984).

Other biotic factors can affect the establishment of seedlings. The importance of the establishment of a mycorrhizal association has been stressed by Baylis (1980). He found that after one season's growth *N. menziesii* seedlings growing in sterilized Podocarp soil ceased to grow at a dry weight of 50 mg. Seedlings grown in untreated beech soil had a dry weight at the end of the season of 500 mg. Baylis considered that these data explained the patterns of seedlings establishment and regeneration observed in *Nothofagus*. He assumed that most soils are deficient in phosphorus, and that the plants obtained phosphorus from the mycorrhizal association. Baylis claimed that the distribution of mycorrhizal fungi determines where beech can grow. However there are no data on the growth of seedlings in unsterilized podocarp soil or sterilized beech soil.

The requirements for water and a suitable light regime limit the areas in which seedlings may become established. Seedlings growing under shaded conditions enter the suppressed phase until the canopy opens or the seedling eventually dies. Seedlings which successfully establish on open sites grow rapidly to enter the sapling stage.

1.6 WATER.

The availability of water to plants is determined by the water content of the soil, and its physical and chemical characteristics. Atmospheric water vapour deficit determines the potential rate of water loss or evaporative demand. Plants have developed several types of adaptations to limit water loss. Two broad groups of adaptation may be defined; morphological and physiological. Examples of morphological adaptations include thick cuticle and stomatal hairs. These features are often found in plants from arid environments. Physiological adaptations limit either water loss, or the damage caused by desiccation. Since the major pathway of water loss in vascular plants is by diffusion through the stomatal apparatus, most plants close stomata to reduce transpiration under certain environmental conditions. Many plants will close stomata when water is limiting or when the potential rate of evaporation is high.

Transpired water vapour and carbon dioxide for photosynthesis both diffuse through stomata and any adaptation that limits water loss will therefore also reduce

photosynthesis. A measure of the efficiency of photosynthesis per unit water loss is the water use efficiency (WUE). Plants growing in arid environments usually have higher WUE than mesophytic species.

Stomatal adaptations limiting water loss vary considerably between plant types. Stomatal closure in response to low plant water potential is being well documented. Closure in response to increasing VPD was demonstrated by Lange *et al.* (1971). In recent years stomatal responses to atmospheric humidity have been widely reported in most types of terrestrial vascular plants. Stomatal responses to water potential and VPD were reviewed by Jarvis and Morrison (1981) and Schulze and Hall (1982).

The role of water potential in determining stomatal conductance is controversial. It was believed for many years that there is a critical water potential which must be exceeded before stomatal closure will occur (e.g. Beadle *et al.* 1978). Several recent studies have however suggested that leaf water potential is not important in regulating stomatal conductance and that instead soil water potential is the controlling factor (e.g. Bates and Hall 1982, Gollan *et al.* 1985, Schulze and Kuppers 1979). Earlier reports of stomatal closure in response to reducing leaf water potential could also be interpreted as responses to soil moisture since almost invariably water potential was manipulated using soil drying treatments. Rapid changes in stomatal conductance can be observed immediately after cutting a twig or branch (Benecke pers. comm.) and because of this results obtained using excised shoots or plants should not be extrapolated to represent whole plants (e.g. Beadle *et al.* 1978).

Water potential acts on photosynthesis indirectly via stomatal effects or by reducing the mesophyll capacity for photosynthesis. Methods which can be used to analyze limitation of photosynthesis have been reviewed by Farquhar and Sharkey (1982) and Jones (1985). Farquhar and Sharkey suggested that in order to demonstrate stomatal limitation of photosynthesis the ratio of the internal to ambient concentrations of carbon dioxide (C_i/C_a) should decrease as stomata close. An analytical method using supply and demand functions has recently shown that reductions in water potential can decrease photosynthetic rates by both stomatal effects (Ehleringer and Cook 1984, Gollan *et al.* 1985) and by reducing photosynthetic capacity (Matthews and Boyer 1984).

Stomatal response to VPD was analyzed by Farquhar (1978) as a mechanism of maximizing WUE in a changing environment. Farquhar's 'feed-forward' hypothesis required that as VPD increased, the transpiration rate should reach a peak and then decline. There are reports of feed-forward responses in some species (Farquhar *et al.* 1980, Mooney *et al.* 1983) but not in all that have been investigated. Plants from arid environments often show a feed-forward response whilst mesophytic plants often do not show a maximum transpiration rate.

Non-stomatal factors which may influence the rate of photosynthesis were reviewed by Schulze (1986).

The sensitivity of stomata to humidity usually declines as the leaf ages (Lange and Meyer 1979, Benecke and Evans 1986) and is higher in sun than shade foliage (Schulze and Hall 1982, Benecke and Evans 1986). Low soil water potentials may increase sensitivity (Osonubi and Davies 1980) though Benecke and Evans (1986) found that *N. truncata* showed greater sensitivity during a moist summer than a drought.

Photosynthetic rates have been observed to decline with increasing VPD as the stomata close. The effect of VPD on photosynthesis is indirect, and mediated by the stomata. The response is often linear (Schulze and Hall 1982, Benecke and Evans 1986) and the sensitivity of photosynthesis to VPD is often less than that of stomatal conductance (Rawson *et al.* 1977).

1.7 LIGHT.

The responses of stomata and photosynthesis to photosynthetically active radiation is well documented (Bjorkman 1981, Schulze and Hall 1982). Stomata of most species open in response to increasing light up to a maximum stomatal conductance. Photosynthesis responds in a similar manner with important features of the curve being the light compensation point, and the maximum photosynthetic rate. The light compensation point for photosynthesis is species and temperature dependent and varies with season (Benecke and Evans 1986). Maximum rates of photosynthesis are species dependent and are related to the light environment and nitrogen content of foliage (Schulze and Hall 1982, De Jong and Doyle 1985). Wong *et al.* (1979) showed that there is often a linear relation between A_{max} and g_s at A_{max}.

The light environment beneath a canopy is modified by the passage of light through several successive layers of foliage. Light intensity is reduced by each layer of foliage and the spectral composition changes with the red/far red ratio decreasing. In addition to the filtered or attenuated light a second component is the direct unfiltered light in sun-flecks which forms a major component of the total daily photon flux. The importance of sun-flecks in determining total assimilation in the sub-canopy has been reported by Pearcy 1983 and Woods and Turner 1971. Both of these studies found that a large proportion of total carbon assimilation occurred during sun-flecks. Adaptations to maximize carbon gain from short periods of high light intensity would be advantageous for sub-canopy plants.

Woods and Turner (1971) found that the rate of stomatal opening in response to increased light intensity was proportional to the shade tolerance of the plant. The response was fastest in highly shade tolerant *Fagus grandifolia* seedlings. Davies and Kozlowski (1974) repeated these experiments and also studied response time to VPD. They found similar results relating response time to shade tolerance.

Transpiration rates were highest in the shade tolerant species indicating that these species had less well developed adaptations to prevent water loss.

1.8 SUPPRESSED SEEDLINGS.

In the shaded conditions under a relatively intact canopy the growth of beech seedlings is suppressed. They become part of an 'advance growth' pool which provides a source of seedlings for stand replacement (Wardle 1984). These seedlings have slow growth rates and after 20 years may be less than 20 cm in height (Wardle 1970, June and Ogden 1975). They remain in the suppressed state until they die or a break in the canopy occurs to which they can respond with increased growth rates. *N. menziesii* is the best example in that its seedlings can persist for long periods under more dense shade than the other species (Franklin 1974) and is assumed to be more shade tolerant (Manson 1974, Wardle 1984).

1.9 SAPLING GROWTH.

Released seedlings or saplings have growth rates many times that of suppressed seedlings in the same area (Wardle 1970, Kirkland 1961) and in a canopy gap or open site grow rapidly to become saplings or poles. This phase is characterized by rapid height growth and strong inter-plant competition. Wilcox and Ledgard (1983) described a provenance trial comparing the four indigenous beech species. They demonstrated appreciable differences in the height and diameter growth rates of seedlings between species and between provenances within species. The fastest growth rates were observed in *N. fusca* and the slowest in *N. menziesii* and high altitude *N. solandri* var. *cliffortioides*. These results confirm those from field observations and management trials (Rennison 1963, N.Z. Forest Service 1980). There has been no experimental work conducted to compare the carbon fixation or partitioning of suppressed and released seedlings.

1.10 BEECH MANAGEMENT.

The beech management systems used in New Zealand were reviewed by Gleason (1982). *N. menziesii* and *N. fusca* are the two *Nothofagus* species which are currently managed in production forestry. The management systems rely upon natural regeneration from seed trees which are left standing during the logging process. This system is similar to those in use with European *Fagus* forests. The system is dependent on successful seedling establishment and survival during the critical early years. Whilst in many areas successful regeneration has occurred, in others partial or total failure has resulted usually from competition with weed species or desiccation (Kirkland 1961, Wardle 1984). As well as problems with establishment there has been widespread death of shoot tips in rapidly growing saplings. No work has been conducted to investigate the physiological causes of these problems. Wardle (1983) produced a paper summarizing the ecological basis for beech management in New Zealand. His analysis was limited by the lack of

information on the processes controlling seedling establishment and early growth of New Zealand *Nothofagus* species. Before advances can be made on understanding the ecological basis for beech management, data is required on regeneration in natural forest and the sub-canopy environment. Comparison with similar data from artificial logged sites would aid in understanding how the environment effects regeneration and why regeneration differs between sites.

1.11 SUMMARY.

Reviewing the literature relevant to *Nothofagus* ecology in New Zealand shows large areas which require further work. The investigation of physiological aspects of growth and development has been limited to a few studies on adult trees, whilst no attempt has been made to study the seedlings phase. Successful regeneration is required if a species is to maintain a presence in the canopy and seedling establishment and subsequent growth is a critical phase during the regenerative cycle. A large proportion of all adult trees growing in a canopy are derived from the pool of suppressed seedlings and would have been released by a break in the canopy cover. Disturbance of a closed canopy would drastically alter the micro-environment which the suppressed seedlings experience. The canopy opening would have two main effects; to increase light intensity, and to increase the atmospheric vapour pressure deficit.

Seedlings growing under a closed canopy tend to have poorly developed adaptations to limit water loss. It is likely that these seedlings would experience severe water stress growing under a opening caused by large scale disturbance of the canopy, and that the stress would would limit successful regeneration to smaller gaps or near the canopy edge.

1.12 AIMS OF THE STUDY.

1. To test the hypothesis that the foliage of *Nothofagus* seedlings growing under a closed canopy has a poorly developed stomatal response to atmospheric water vapour pressure deficit, and that the lack of stomatal control of transpirational water loss limits successful regeneration to beneath small canopy gaps or to near the canopy edge.

2. To use the physiological information obtained in this study to improve our understanding of the processes influencing *Nothofagus* regeneration, and to relate this to the management of both natural and production forest.

2. GAS EXCHANGE METHODS.

2.1 INTRODUCTION.

Gas exchange systems utilize indirect methods to estimate the rates of transpiration and net photosynthesis or assimilation. Characteristics of the different systems used for gas exchange measurements have been reviewed by Smith and Hollinger (1987). Their design is based around a chamber or cuvette enclosing the foliage to be measured. Rates of net photosynthesis and transpiration are measured from fluxes of CO_2 and water vapour around the leaf. CO_2 concentration is usually measured by infra-red gas analysis (IRGA), and water vapour using IRGA, dew point mirrors, or humidity sensors. There are three main groups of system currently used; closed, semi-closed, and open (Jarvis *et al.* 1971).

2.1.1 Closed systems.

In a closed system the rate of gas exchange is estimated by the change in CO_2 and water vapour concentration in the leaf chamber over a measurement period. These systems have a major inherent problem in that the conditions within the chamber vary continuously during the measurement period as the concentration of CO_2 decreases and water vapour increases. Another problem with closed systems is that the gas path must be sealed and that they are particularly sensitive to errors in transpiration measurements due to water adsorption. These problems have meant that closed systems are usually used with short measurement periods or to determine CO_2 compensation points. The main advantages of closed systems are that the design is simple, they are inexpensive and easy to build, and that they can be made more portable than other systems.

2.1.2 Semi-closed systems.

The semi-closed system is a development of the closed system which regulates the concentration of CO_2 and water vapour in the chamber. The CO_2 concentration is controlled by adding a measured supply of CO_2 or CO_2-free air to the chamber. The rate of photosynthesis is estimated from the amount of CO_2 added. Transpiration rates are estimated using the same method with either dry or moist air added to maintain the water vapour concentration in the system. The design of a semi-closed system provides a means of controlling the composition of the air within the leaf chamber. This facility when combined with temperature control of the chamber can be used to determine factor responses for CO_2, VPD and temperature. The main disadvantage of semi-closed designs is that they are more complex and expensive to construct than closed systems.

2.1.3 Open systems.

In an open system gas exchange is measured by passing a stream of air of known composition through the cuvette. The concentrations of CO_2 and water vapour are measured in the air leaving the chamber with photosynthesis and transpiration being proportional to the concentration difference and the flow rate. Open system designs provide the best means of controlling the composition of the air within the leaf chamber. They can be used to study the effects of other gaseous compounds on leaf gas exchange, which is useful in pollution studies. The disadvantages of open designs are that they can be the most complex and expensive to build and they are expensive to run if the air composition is controlled.

2.2 GAS EXCHANGE CALCULATIONS.

2.2.1 Flux calculations.

Cowan (1977) suggested that gas exchange calculations should utilize molar units rather than the mass units used previously. Molar units expressed on an area basis are now consequently widely used. The formulae used to calculate flux depend on the type of gas exchange system, and are derived from the ideal gas law.

2.2.2 Conductance calculations.

Stomata represent the major pathway for the diffusion of CO_2 and water vapour between leaf and the atmosphere. Stomatal conductance is a measure of the stomatal limitation of photosynthesis and transpiration. Low conductance values indicate closed stomata with values increasing as stomata open. Estimates of stomatal conductance are obtained using a resistance analogue model to remove the boundary layer conductance from measurements of leaf conductance. Leaf conductance to water vapour is estimated using Fick's Law of Diffusion by dividing the transpiration rate by the leaf-air vapour pressure deficit. Stomatal conductance to CO_2 diffusion is calculated from the conductance to water vapour (von Caemmerer and Farquhar 1981). These calculations ignore the effects of cuticular conductance.

2.2.3 Internal carbon dioxide concentration.

The internal CO_2 concentration (c_i) can be estimated from measurements of photosynthesis and transpiration. The CO_2 concentration difference between the mesophyll and ambient air is proportional to the photosynthetic rate divided by the leaf conductance to CO_2 (von Caemmerer and Farquhar 1981). Indirect estimations of C_i have been validated using direct measurement by Sharkey *et al.* (1982).

2.3 LI-6000 PORTABLE PHOTOSYNTHESIS SYSTEM.

The gas exchange system used in this study was the LI-COR LI-6000 portable photosynthesis system (LI-COR inc., Lincoln, Nebraska, USA). It was initially designed as a closed circuit system, but was later modified by LI-COR to include a manually operated by-pass water vapour trap. The LI-6000 uses an internal microprocessor to record and store data, as well as to compute estimates of gas exchange parameters after each measurement has been completed. CO_2 concentration was measured using an IRGA working on an absolute scale with software correction to linearize the response. The air stream passed through a water vapour trap before entering the IRGA to reduce measurement cross-sensitivity.

The water vapour by-pass used magnesium perchlorate to dry the air stream before it passed through the IRGA and was returned to the chamber. The transpiration and conductance calculations assume that the air returning to the chamber had a water vapour pressure of zero. In the first season of operation (1984-5) the flow rate was fixed, and was assumed to be constant by the software. The by-pass system was modified by LI-COR in June 1985 to allow a variable flow rate measured by a mass flow meter.

All measurements is this study used a four litre chamber manufactured by LI-COR. The leaf chamber was constructed from polycarbonate and in the second season of operation (1985-86) was lined with teflon to reduce the effects of water adsorption. The chamber contained two fans to assure adequate mixing of the air sample. The foliage was positioned horizontally in the center of the chamber between two sets of parallel monofilament lines and leaf temperature was measured by a thermocouple appressed to the underside of a leaf. Relative humidity was measured in the leaf chamber using a Vaisala capacitance type humidity sensor and the water vapour concentration calculated using chamber air temperature as measured by a thermistor temperature probe. Photosynthetically active photon flux density (PPFD) was measured by a LI-COR LI-190 quantum sensor attached outside the chamber. Measurement errors were usually less than ten percent for the estimates of transpiration, photosynthesis and stomatal conductance and twenty percent for internal CO_2 concentration (LI-COR 1985).

The LI-6000 uses a microprocessor to make rapid, repeated measurements in an effort to reduce the problems associated with closed systems. The gas exchange parameters are calculated using a series of measurements from each sample. Up to ten measurements per sample are recorded and stored together as a 'page' of data. Point estimates of photosynthesis, transpiration and stomatal conductance are calculated for each successive pair of measurements in a page and the photosynthesis and conductance estimates are stored by the system. The built-in software calculates a linear regression against time to estimate the initial value of each measured and computed variable. The mean and range are also calculated. The LI-6000 estimates the initial internal CO_2 concentration, and transpiration rate using the regression intercepts.

2.4 LI-6000 FORMULAE

The software implemented on the LI-6000 was originally limited by available memory (J. Welles pers. comm.) and does not fully implement current formulae (e.g. those of von Caemmerer and Farquhar 1981). For this reason alternative formulae were developed for the LI-6000 and implemented in a computer programme to provide a customized data analysis system for the LI-6000. The alternative formulae closely resemble those used in the LI-6000 except for major differences in the by-pass calculations.

2.4.1 Photosynthesis.

Photosynthetic rates are calculated from the change in the molar concentration of CO_2 in the system over the time period t_i to t_f using the ideal gas law.

$$A = \frac{PV}{Ra(t_f - t_i)} * \left[\frac{[C_i]}{T_i} - \frac{[C_f]}{T_f} \right] \qquad \text{(eqn. 2.1)}$$

where:-

A	=	assimilation rate	(μmol m^{-2} s^{-1})
P	=	atmospheric pressure	(Pa)
V	=	system volume	(m^3)
R	=	universal gas constant	(J mol^{-1} K^{-1})
a	=	leaf area	(m^2)
t_f	=	time at end of measurement	(s)
t_i	=	time at start	(s)
$[C_f]$	=	CO_2 concentration at end	(μmol mol^{-1})
$[C_i]$	=	CO_2 concentration at start	(μmol mol^{-1})
T_f	=	air temperature at end	(K)
T_i	=	air temperature at start	(K)

2.4.2 By-Pass Calculations.

The instantaneous rate at which the concentration of a gas in a semi-closed system changes due to the action of a by-pass is a function of the system volume, by-pass flow rate and the concentration difference between the input and output of the by-pass.

$$n = f(F,Q,q,T) \qquad \text{(eqn. 2.2)}$$

where:-

n	=	Rate of change	(mol s^{-1})
F	=	By-pass flow rate	(m^3 s^{-1})
Q	=	return vapour pressure	(Pa)
q	=	Ambient vapour pressure	(Pa)
T	=	Gas temperature	(K)

using the ideal gas law, the function can be defined as;

$$n = \frac{F(q-Q)}{RT} \qquad \text{(eqn. 2.3)}$$

In an ideal steady state system, the parameters of the function would remain constant over the period of measurement and the total change due to the by-pass is obtained by integrating equation 2.3 over the period t_i to t_f. This gives an equation equivalent to that used by Kuppers (1984).

$$N = \int_{t_i}^{t_f} \frac{F(q-Q)}{RT} = n\,(t_f - t_i) \qquad \text{(eqn. 2.4)}$$

where:-

N = total change due to by-pass (moles)

In practice the conditions within the system will change over the measurement period. The calculation of transpiration is dependent on an accurate estimate of the effect of a by-pass in the system. If the environmental conditions change during the period of measurement, the value of N is obtained by integrating the general equation 2.2.

$$N = \int_{t_i}^{t_f} f\,(F,Q,q,T) \qquad \text{(eqn. 2.5)}$$

The solution of equation 2.5 requires a knowledge of the energy balance, and the nature of variation in F, Q, q, and T with time over the period t_f to t_i. The solution can be simplified if it is assumed that the derivative ($^{dn}/_{dt}$) is constant. The use of this assumption requires that changes in F, Q, q, and T should be small during the measurement period. In practice this is met by using short measurement periods of between one and twenty seconds, and by attempting to maintain the chamber conditions relatively constant. Using this assumption, a simple by-pass equation can be obtained (eqn. 2.6).

$$N = \tfrac{1}{2}(n_f + n_i)(t_f - t_i) \qquad \text{(eqn. 2.6)}$$

where:-

$$n_i = \frac{F_i(q_i - Q_i)}{RT_i}$$

$$n_f = \frac{F_f(q_f - Q_f)}{RT_f}$$

q_i	=	vapour pressure at start	(Pa)
q_f	=	vapour pressure at end	(Pa)
n_i	=	amount removed at start	(moles)
n_f	=	amount removed at end	(moles)

This equation simplifies to equation 2.4 if the environmental conditions are constant. The by-pass calculations built into the LI-6000 have been derived from equation 2.3 but use different assumptions. The LI-6000 formulae assume that the system is closed with no external input of water vapour, and that the vapour pressure decreases during the measurement due to the by-pass. By integrating equation (2.3) over the period (t_i to t_f) it is possible to predict the change in water vapour pressure (dq) due to the by-pass, if the vapour pressure (q_i) at t_i is known (equation 2.7).

$$dq = (q_i - Q)(1 - e^{-b})$$

where

$$b = \frac{F}{V}(t_f - t_i) \qquad \text{(eqn. 2.7)}$$

dq	=	change due to by-pass	(Pa)

(LI-COR, 1985)

2.4.3 Transpiration.

Transpiration rates are calculated internally in the LI-6000 by adding dq (eqn 2.7) to the measured change of water vapour pressure during the measurement period (eqn. 2.8). If equation 2.6 is used to calculate the effect of the by-pass, the transpiration rate is then determined by equation 2.9. When there is no foliage in the chamber equations 2.8 and 2.9 are equivalent. Equation 2.8 will underestimate the amount of water removed by the by-pass when foliage is placed in the chamber.

(eqn. 2.8)

$$E_{t(LI\text{-}COR)} = \left[\frac{(q_f+dq)}{T_f} - \frac{q_i}{T_i} \right] * \left[\frac{V}{a\ R\ (t_f - t_i)} \right]$$

where:-

E_t = Transpiration rate (mol m^{-2} s^{-1})

(eqn. 2.9)

$$E_{t(Alt)} = \frac{\left[\frac{V}{R} * \left[\frac{q_f}{T_f} - \frac{q_i}{T_i} \right] + N \right]}{a\ *\ (t_f - t_i)}$$

where:-

N = by-pass effect (eqn. 2.6) (moles)

$E_{t(Alt)}$ = Alternative transpiration calculation. (mol^{-2} s^{-1})

The magnitude of the difference between the alternative by-pass formulae and those used by LI-COR depends on the system volume (V), by-pass flow rate (F), the logging interval ($t_f - t_i$) and the difference between the initial and final vapour pressures in the system ($q_f - q_i$). A formula giving a rough estimate of the difference is given in equation 2.10 which also applies to stomatal conductance. Figure 2.1 shows actual percentage differences for selected examples calculated using equations 2.8 and 2.9.

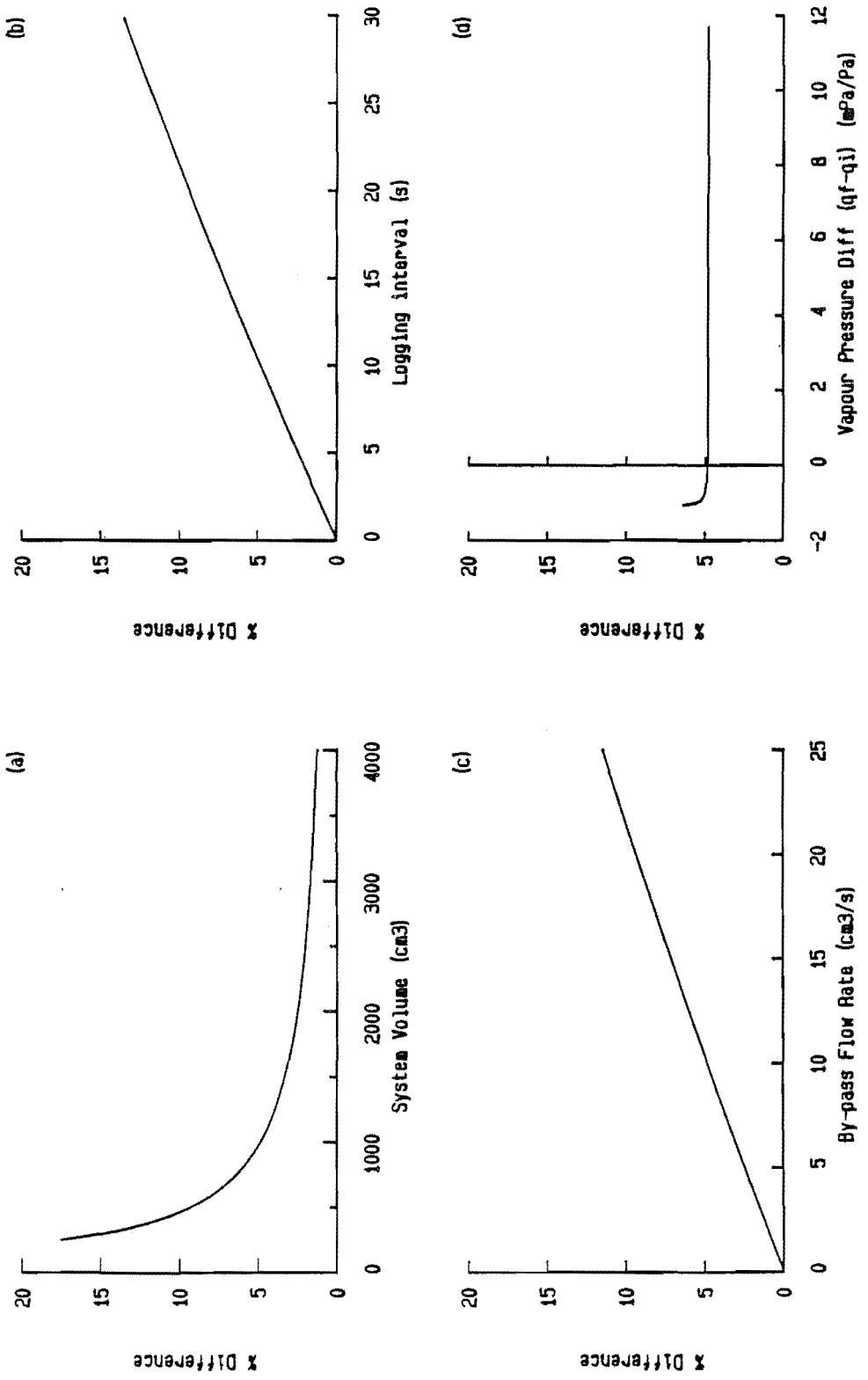

Figure 2.1 Differences between By-pass calculations.

The percentage difference between eqns. 2.8 and 2.9 with standard conditions of a one litre chamber, by-pass flow rate of 10 cm s^{-1}, 10 s logging interval and constant water vapour pressure.

(a) Effect of system volume.

(b) Effect of logging interval.

(c) Effect of by-pass flow rate.

(d) Effect of a change in vapour pressure (q_f-q_i) during the measurement period.

(eqn. 2.10)

$$\%Diff \approx \frac{[E_{t(Alt)} - E_{t(LI-COR)}]}{E_{t(Alt)}}$$

$$\approx \frac{[(t_f - t_i) - V/F(\ 1 - e^{-b}\ )] * 100}{(t_f - t_i)}$$

where b is defined in eqn.2.7.

2.4.4 Stomatal conductance.

Stomatal conductance is calculated from the transpiration rate (eqn. 2.9) using standard formulae (von Caemmerer and Farquhar 1981). The formulae include a correction for the effect of mass flow of water vapour from the leaf (Jarman 1974). Stomatal conductance is calculated by removing the effects of the boundary layer using the formulae derived by LI-COR (1985). The boundary layer conductance for *N. menziesii* and *N. fusca* was determined with twigs coated in plaster of Paris (Landsberg and Ludlow 1970). The value for *N. menziesii* was 1000 mmol m^{-2} s^{-1} and for *N. fusca* 1400 mmol m^{-2} s^{-1}.

3. COMPUTATIONAL METHODS.

3.1 INTRODUCTION.

The LI-COR LI-6000 portable photosynthesis system was one of the first commercial, portable systems to use a microprocessor for system control and data storage. The system collects large volumes of data which are stored in internal memory until transfer to a host computer for analysis. A computerized system for data analysis is required because of the large amounts of data produced.

Data are stored in the LI-6000 as a group of pages, each representing a series of up to ten point measurements on the same leaf or twig. The software built into the LI-6000 is designed to compute data after each page is measured and displays computed gas exchange parameters within 20 seconds. This allows the operator to monitor results for aberrant data and to take corrective steps. The major weakness of the LI-6000 software is that there is no method to analyze data after collection except by loading data back into the LI-6000.

A set of programs were developed during this project to process data from the LI-6000 on IBM PC or compatible computers . The software:-

1. provides fast and accurate data transfer to a host computer.
2. removes the need to load data back into the LI-6000 for data analysis.
3. emulates and improvesthe gas exchange formulae built into of the LI-6000.
4. provides a software interface to statistical and graphics programmes.
5. computes multivariate models for gas exchange data.

Hardware requirements. The programmes require an IBM PC, XT, AT or fully compatible with at least 256 Kbytes of memory and a standard asynchronous communications adapter (RS232). The programme will run with one diskette drive, but the use of two drives is advised. All programmes were written in Microsoft Pascal and assembler and feature full support for a 8087 or 80287 maths co-processor if fitted.

Programme use. The programmes assume only a very basic level of computer literacy and are easy to use for first time computer users. The programmes accept LI-6000 data files and limit command selections so that they are unlikely to fail. The programmes display menus of options on the screen which are selected using single key commands.

3.2 DATA TRANSFER.

The software built into the LI-6000 transfers stored data to host computers either as text, or as a binary memory dump. The text format is used to output data to a printer, screen, or to a disk file for permanent storage. A computer programme to handle text output is easily implemented on most computers. The rate of transfer can be very slow taking up to 15 s per page if already computed and 30 s if not. A binary dump is rapid taking up to 6 s per page, and is more accurate since an error checking routine is used. Binary data has the additional advantage that it can be loaded back into the LI-6000 if required. The disadvantages of binary transfer is that the computer programme required to process binary data is more complex, and that the data requires conversion before information can be output to a screen or printer.

The communications software that was developed during this project for IBM PC compatible computers transfers data from the LI-6000 to the host PC for storage and further analysis. Data is transferred at 4800 baud (480 characters per second) which is the maximum speed supported by the LI-6000. Transfer of binary data is supported with full error checking and the ability to re-load data into the LI-6000. Using this software it is now possible to transfer a copy of the full memory of a 32K LI-6000 to the PC in less than five minutes compared with up to thirty if text format is used.

3.3 DATA COMPUTATION.

Data stored on the PC can be analyzed without needing to be re-loaded into the LI-6000. Two programmes have been developed which both use special random access data files. The random access files are created from binary or textual data using a conversion programme. The programmes typically take less than two seconds to compute a page of data compared with fifteen on the LI-6000.

The software uses formulae derived in chapter 2 which are similar to those used in the LI-6000. Molar units are used internally, (Cowan 1977) but the software will convert to mass units if required. The alternative by-pass calculation is used by default, with an option to use LI-COR's if required. The software stores an estimate of the initial leaf-air vapour pressure deficit (VPD) in the page header, and calculations of the internal CO_2 concentration have been corrected for mass flow effects (Jarman 1974) according to the formulae of von Caemmerer and Farquhar (1981).

A batch programme is used to compute all the pages in a file after setting user selected parameters at appropriate values. This programme is useful when processing the data for the first time. It can for example be used to set the correct leaf areas for each page in the file using a list of leaf areas entered by the user. The leaf area option is the one most frequently used since areas are usually

measured after the gas exchange measurements have been completed. Using the batch programme to compute a file of 100 pages typically takes less than 5 minutes compared with a similar exercise on the LI-6000 taking an hour.

The full screen editor is useful for making changes to selected pages of data in a file. This programme is useful in two situations. The first is for conducting 'what if' analyses. The editor can be used to determine the effect of changing a parameter by altering its value and then re-computing the page. The second is to remove data from a file. Occasionally the LI-6000 will record erroneous data if for example the CO_2 analyzer is bumped, or a cloud covers the sun during a measurement. The gas exchange parameters calculated from such data will be biased and should not be used. The editor is used to remove such data from a page and or make the page unavailable to the data analysis programmes.

The LI-6000 computes summary statistics for each page of data. The page is split into three logical areas. The header stores information such as the leaf area and atmospheric pressure which apply to the page as a whole. In the observation area measured data such as leaf temperature or ambient CO_2 concentration are stored with the computed estimates of the stomatal conductance and photosynthetic rate. The summary area stores the mean, standard error and range of each measured and computed variable. The LI-6000 computes a regression line for each measured and computed variable against an independent variable of time. The regression line is used to calculate an initial value (Y intercept) and standard error which are stored with the other summary statistics.

The use of an initial value of a variable assumes that changes occur in a linear fashion with time. Tests with the system (Fig. 3.1) have shown that this assumption is not always true. The use of the initial value instead of the mean when the slope of the regression is not significant increases the experimental error. The software developed during this project calculates an F test on the slope of the regression equation, and stores the value of F with the observations. In this study the mean was used as the estimate of all computed variables except internal CO_2 concentration.

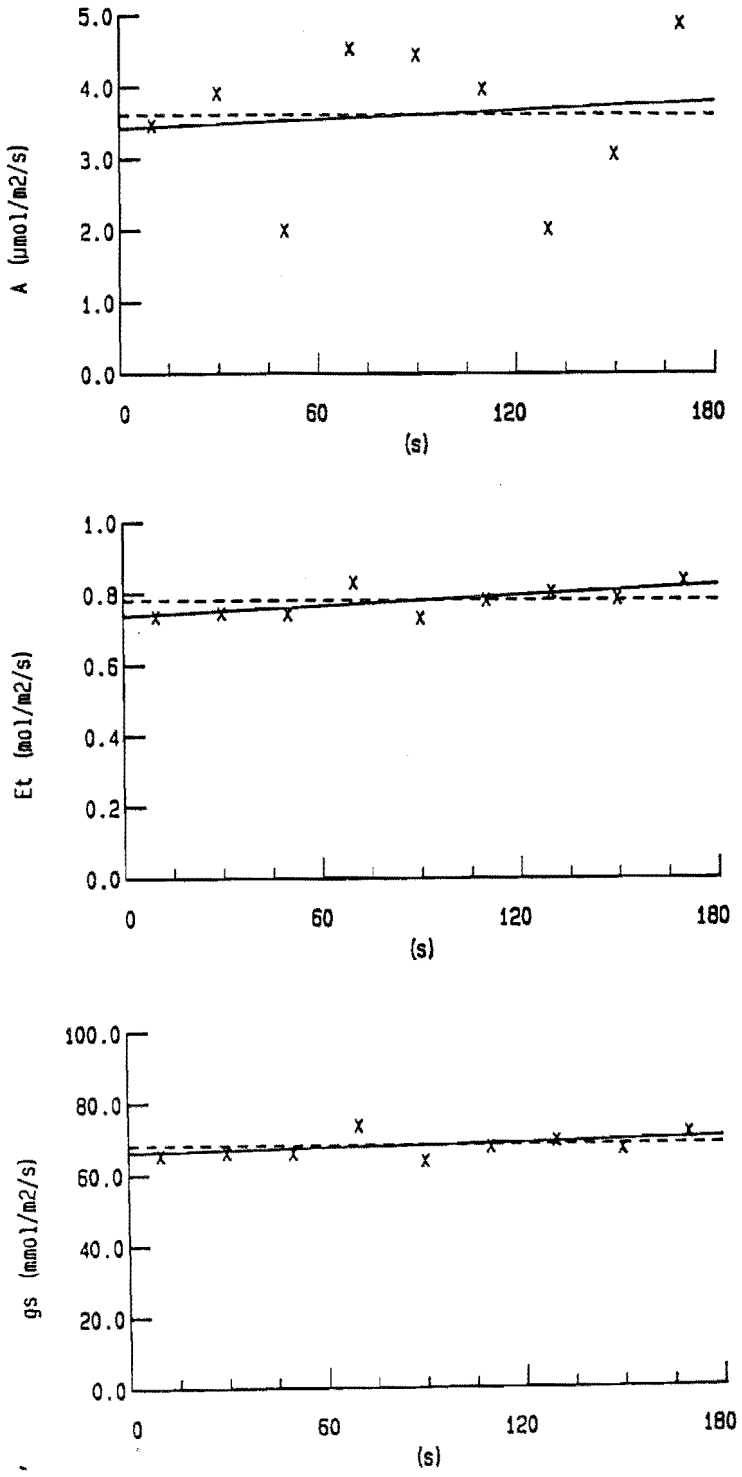

Figure 3.1 Time course of gas exchange measurements obtained using the LI-COR LI-6000 portable photosynthesis system.

Estimates of the rates of photosynthesis (A), transpiration (Et) and stomatal conductance (g_s) were calculated using the computer programme described in this chapter. The solid line represents the regression equation for each computed variable against time. The slope of the regression equations were not significantly different from zero as determined by analysis of variance. The intercept of the regression lines with the dependent axis represents the 'initial value' as calculated by the LI-6000. The dashed lines pass through the mean of each computed variable.

3.4 DATA ANALYSIS.

3.4.1 Introduction.

A major problem with porometry is the development of appropriate methods for the analysis of field data. Data from field studies are characterized by several environmental factors varying continuously during the day (Fig. 3.2). In order to determine the photosynthetic or stomatal responses to environmental parameters, these responses must be separated from the measurement error term. Another problem with field data is that two or more factors may interact in such a way that obscures the response to one factor on its own. An example of this can often be observed when determining stomatal response to light. If the assimilation data in Fig. 3.2 are plotted against an independent axis of light little or no response is observed (Fig. 3.3). The reason for the apparent lack of light response is that as light intensity varies during the day VPD changes in a similar manner. The increase of photosynthetic rate in response to increasing light intensity combined with stomatal closure due to increasing VPD and the resulting response appears flat.

The response of plants to environmental factors can be shown in a simple model. If the plant responds to N different environmental variables ($V_1..V_n$) and it is assumed that there are no interaction terms, then the response (Q) is a function :-

$$Q = f\ (V_1,V_2,..V_n) + e \qquad \text{(where } e \text{ is the experimental error)}$$

There are a number of analytical methods which have been used to determine the response of plants to environmental parameters using porometry data. The methods can be divided into two general types. Grouping methods reduce variation by splitting the data into a series of smaller groups based upon narrow ranges of one or more environmental factors. Modelling methods use regression techniques to fit multi-dimensional models to the data set.

3.4.2 Grouping methods.

These methods split a large data set into a series of smaller groups each based upon a narrow range of one or more environmental parameters. Hutmacher and Krieg (1983) used this method to analyze the relationship between stomatal conductance and assimilation in cotton. They split the data into several temperature ranges and fitted separate quadratic functions to the data in each group. Benecke and Havranek (1980a) analyzed the photosynthetic and stomatal response to temperature of trees growing at timberline over several ranges of VPD. They used an additional constraint that light was above saturation point.

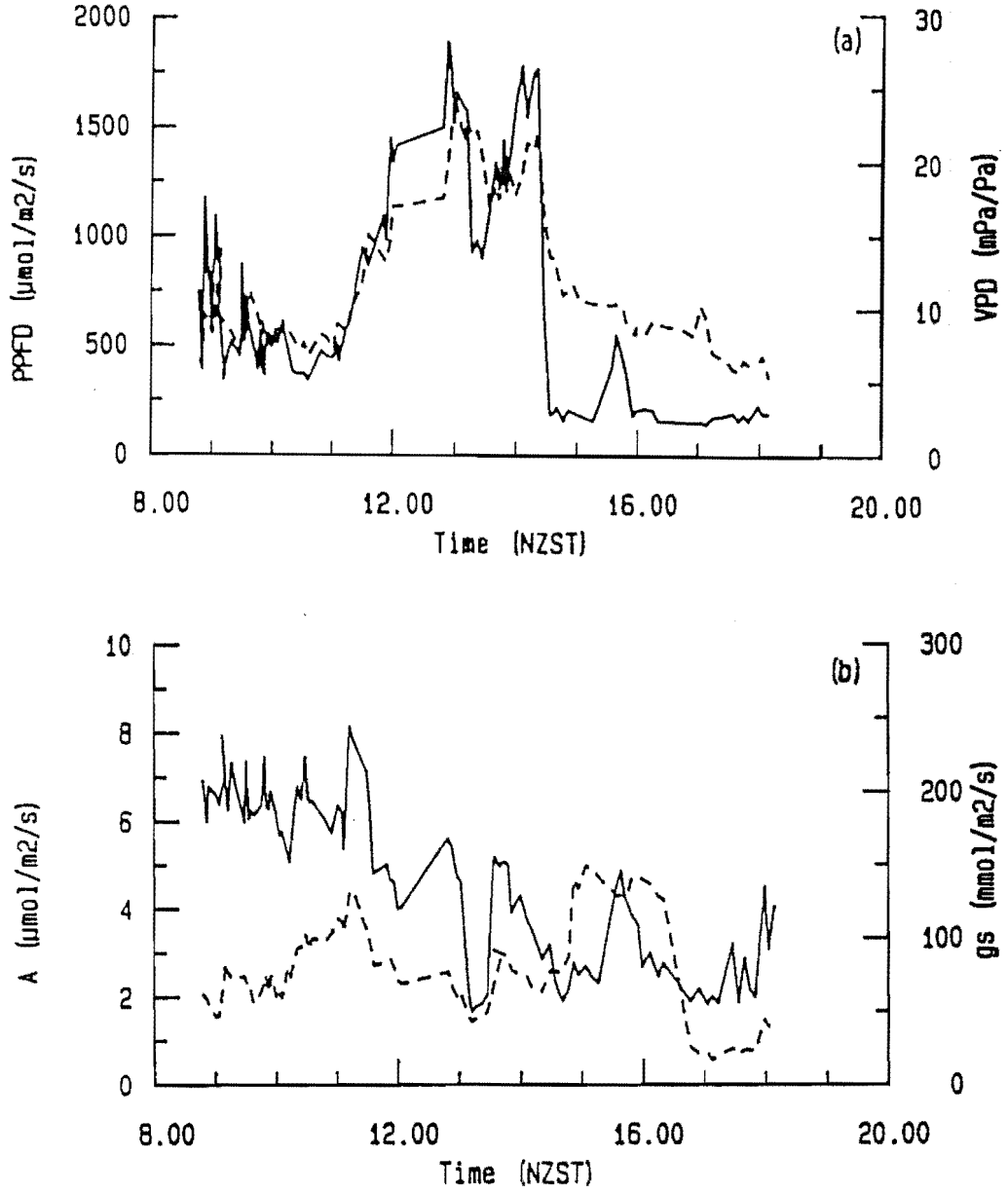

Figure 3.2 Daily time course of environmental parameters and leaf gas exchange for *N. fusca* saplings growing at the FRI Rangiora Nursery on the 17th. of January 1985.

Gas exchange measurements were obtained using the LI-COR LI-6000 portable photosynthesis system as detailed in chapter 5.

(a) Photosynthetically active photon flux density density (PPFD, solid line) and leaf-air vapour pressure deficit (VPD, dashed line).

(b) Photosynthetic rate (A, solid line) and stomatal conductance (gs, dashed line).

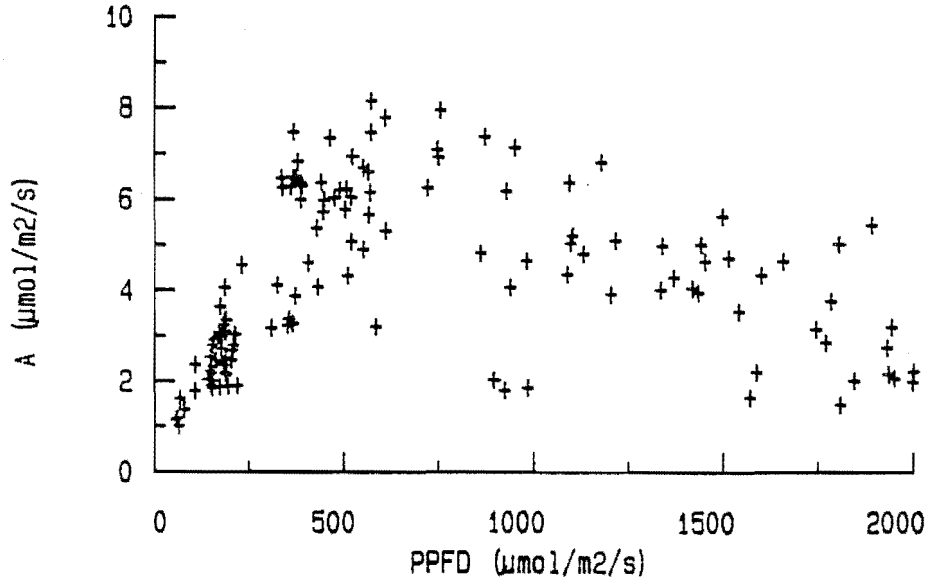

Figure 3.3 Scatter diagram of photosynthetic rate against PPFD.

The data were collected from *N. fusca* saplings as for Fig. 3.2 and include data collected on the 16th. of January 1985.

Hellkvist *et al.* (1980) used a further development of this procedure to produce isometric histograms by sorting porometry data into groups based upon two environmental parameters. The mean of each group was used to represent the response. This method was used to analyze photosynthetic data obtained at Rangiora with *N. fusca* (Fig. 3.4). The analysis was effective in reducing variation within groups giving a coefficient of variation of less than 5% in most groups.

The problem with a two-factor sorting routine is that there is no quantitative way to determine factor responses or to compare results between species or seasons. Grouping methods require a large database before they can be used effectively. It is often difficult to obtain enough data without including seasonal or ontogenetic variation. Another problem with these methods is that it is difficult to obtain representative estimates of plant response to selected environmental factors. If a one-factor sort is used a separate regression analysis is required for each response. This for example would produce a regression equation for the response of stomatal conductance to VPD in four light regimes and for the light response at four ranges of VPD. If a two-factor sort is used quantitative comparisons cannot be made. Sorting methods are a useful first approach to understanding plant response from porometry data. They are not suitable for use as a quantitative method of comparing plant responses in complex environments.

Boundary line analysis (Webb 1972) has been used in the past in several studies (e.g. Pezeshki and Hinckley 1982) to estimate the probable maximum response to an environmental factor assuming that all others are non-limiting. This technique can be considered as a development of a sorting technique. To model a photosynthetic light response the data are sorted into narrow ranges from which the maximum values are selected, with an additional constraint that as light intensity increases the photosynthetic rate must increase. Non-linear regression techniques are then used to fit an appropriate model to the selected data. The boundary line analysis can be criticized because it tends to use outliers from the data and is thus statistically biased. The use of this technique has declined in recent years with most studies now tending to use more complex multi-factor models.

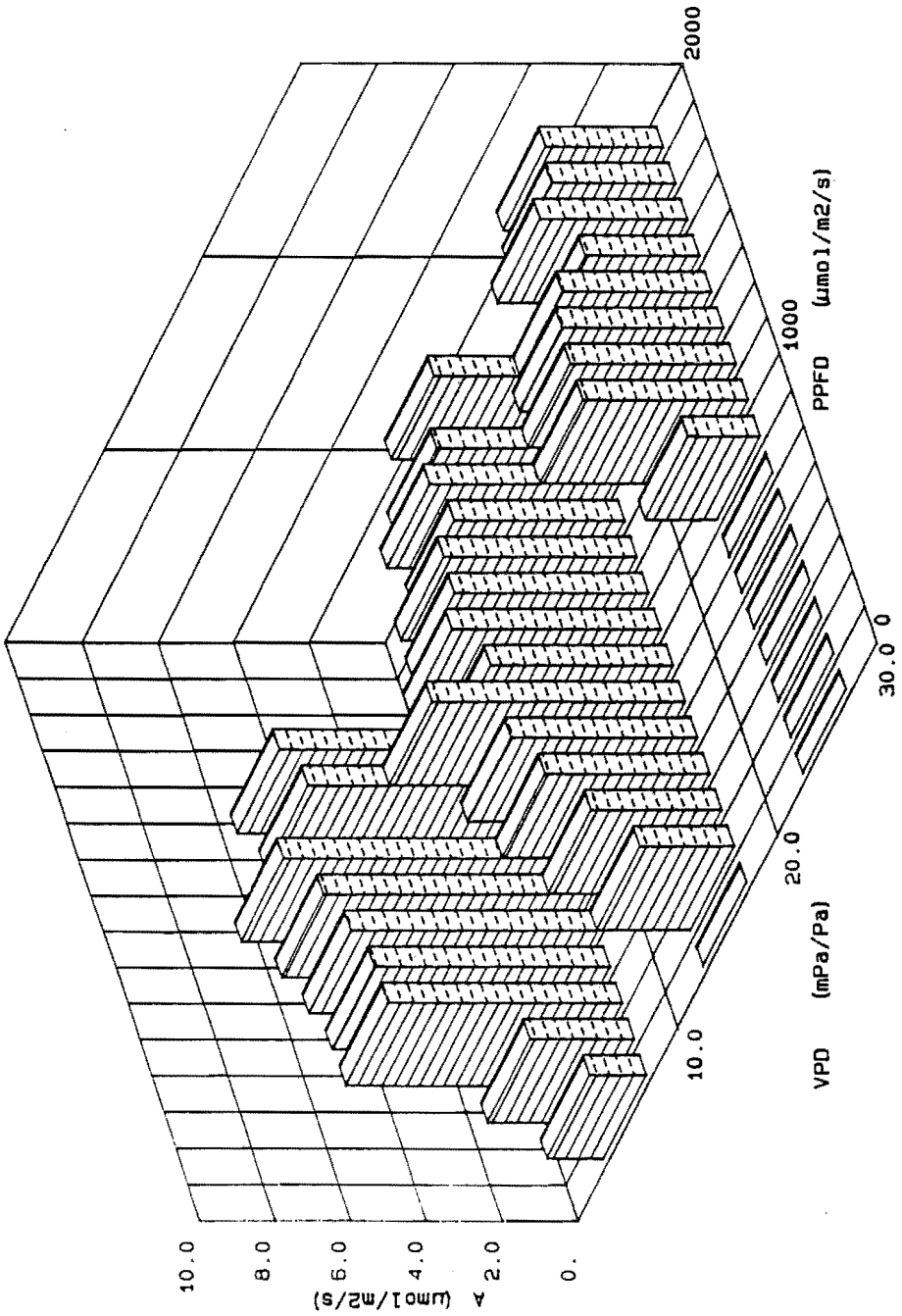

Figure 3.4 Two factor sort of the photosynthetic data from Fig. 3.3 using PPFD and VPD.

The data were sorted into groups based on intervals of 10 mPa Pa^{-1} VPD and 125 μmol m^{-2} s^{-1} PPFD.

3.4.3 Modelling methods.

The applications of mathematical models in plant physiology was reviewed by Thornley (1976). A model can be used to simplify a complex system but should include the essential characteristics of the real system. The use of a mathematical model to analyze stomatal response to the environment was described by Jarvis (1976). His model analyzed stomatal response in relation to the multiplicative sum of the effects of light, VPD, temperature, leaf water potential and ambient CO_2 concentration. A similar model for photosynthesis was described by Reed *et al.* (1976) Both models contain a separate sub-model for each environmental parameter. These models were used as analytical tools to compare plant response to the environment and are thus descriptive or empirical. Mechanistic models for leaf gas exchange are based upon actual biochemical and physical processes. Mechanistic models for photosynthesis and stomatal conductance have been described by Farquhar and von Caemmerer (1982) and Farquhar and Wong (1984).

The appropriate model for use in any study is determined by the aims of the study and by the nature and limitations of the data. The use of multifactor models requires complex regression techniques. Jarvis (1976) discussed the use of non-linear least squares regression in modelling plant response. He stated that to obtain unbiased regression coefficients the data should be uniformly distributed throughout the variable space. This objective is only achieved with climatized systems. Porometer systems operating under ambient conditions do not produce uniformly distributed data and are therefore not ideally suited to multiple regression analysis. These techniques can only be applied to such data with the understanding that the parameter estimates will be biased. The errors associated with fitting a model to a biased data set means that it is only appropriate to use relatively simple descriptive models with ambient porometry data.

A number of recent porometry studies have utilized regression techniques to describe a complex data set. The studies by Warrit *et al.* (1980) and Thorpe *et al.* (1980) used a simple model relating stomatal conductance of apple leaves to light intensity and VPD. Meinzer (1982) used a similar model to analyze the water use efficiency of *Pseudotsuga menziesii* leaves. Kaufmann (1982a) related the stomatal conductance of four tree species to light intensity and VPD using a complex descriptive model. Kaufmann restricted the data to remove any collected during periods of high light variability or low VPD. The low VPD data were removed because of the possibility of dew formation in the system.

The descriptive models used in the above studies had sub-models for the separate effects of light and VPD. Thornley (1976) listed several commonly used descriptive models for the light response of photosynthesis. The two which have been most frequently used are the rectangular hyperbola (eqn. 3.1) and an exponential equation (eqn. 3.2).

$$A = \frac{A_{max}\, Q}{(B + Q)} \qquad \text{(eqn. 3.1)}$$

Where A is the assimilation rate, A_{max} is the asymptotic value of A as Q approaches infinity, Q is the light intensity and B is a constant representing the light intensity at which $A = {}^{1}/_{2}\, A_{max}$

$$A = A_{max}(1 - e^{-CQ}) \qquad \text{(eqn. 3.2)}$$

Where C is a constant representing degree of curvature.

These two equations are simplistic and can be criticized on several grounds. Neither curve includes an estimate of the light compensation point or allows for temperature effects. The initial curvature of a rectangular hyperbola is steeper than the exponential and gives a better fit in the low light region for many species. The exponential reaches saturation at lower light intensities than the hyperbola and tends to give more realistic estimates of A_{max}. These same models can be used to analyze stomatal response to light. The analysis produces an estimate of the maximum stomatal conductance g_{max}.

The responses of stomatal conductance and assimilation to VPD have been modelled using two simple formulae. Both models assume a reduction in g or A as VPD increases. The models assume that there is no synergistic effect between light and VPD. The light model is multiplied by the VPD model to give the net assimilation rate. A linear reduction with increasing VPD (eqn. 3.3) was assumed by Jarvis (1976) and Thorpe *et al.* (1980).

$$A = A_0 (1 - D_A V) \qquad \text{(eqn 3.3)}$$

Where A_0 is the rate of assimilation at zero VPD, V is the VPD, and D_A is the relative sensitivity to VPD. Meinzer (1982) and Kuppers and Schulze (1985) used a negative exponential model (eqn. 3.4).

$$A = A_0 e^{-EV} \qquad \text{(eqn. 3.4)}$$

Where E is an estimate of stomatal sensitivity.

Gas exchange systems cannot measure transpiration or stomatal conductance at low VPD due to the problem of water vapour condensation on surfaces. This

limitation has been recognized by Benecke and Evans (1986) who allowed for the uncertainty at low VPD by calculating an Y intercept at 4 mPa Pa^{-1} VPD rather than 0 VPD. Meinzer (1982) used an offset of 5 mPa Pa^{-1} is his model of water use efficiency.

3.4.4 Residual Analysis.

When a model has been selected for a study the ability of the model to describe the variation in the data must be determined. The coefficient of determination (R^2) represents the amount of variation explained by the regression equation. A good model should explain a high proportion of the variability but a high R^2 value should not be the sole criterion for selection. Jarvis (1976) used a plot of the regression residuals against selected environmental parameters to examine the fit of his model. An appropriate model with non-biased data should give randomly distributed residuals. Kaufmann (1982b) used a plot of residuals to examine the effects of a temperature parameter not included in his model. The residuals were not randomly distributed showing that his first model was not appropriate. Reed *et al.* (1976) used a plot of residual against the measured value of the dependent axis to show the relationship between actual and predicted values in their photosynthesis model.

3.5 MODEL USED IN THIS STUDY.

The aims of the field gas exchange measurements in this study were to obtain estimates of the maximum rates of photosynthesis and stomatal conductance, as well as the sensitivity of stomata to VPD. A model (eqns. 3.5 & 3.6) is used to describe photosynthesis and stomatal conductance in terms of light and VPD. The light response is described by eqn. 3.2 and the VPD response by eqn. 3.3. The exponential form of the light response curve was selected because this formula gives a more realistic estimate of A_{max} and g_{max}. The VPD term is based on a linear decrease in A or g as VPD increases. The maximum rates were defined at a VPD of 5 mPa Pa^{-1}.

$$A = A_{max}(1 - e^{-CQ}) [1 - D_A(V-5)] \qquad \text{(eqn. 3.5)}$$

$$g = g_{max}(1 - e^{-CQ}) [1 - D_g(V-5)] \qquad \text{(eqn. 3.6)}$$

These two models have been applied to porometry data collected under ambient conditions in the field. The models were fitted using a non-linear least squares regression procedure based upon the programme described by Conway *et al.* (1970). Observations with low VPD (less than 5 mPa Pa^{-1}) were removed before analysis since these data often included dew effects. Variable light data were also removed before data were used with the models.

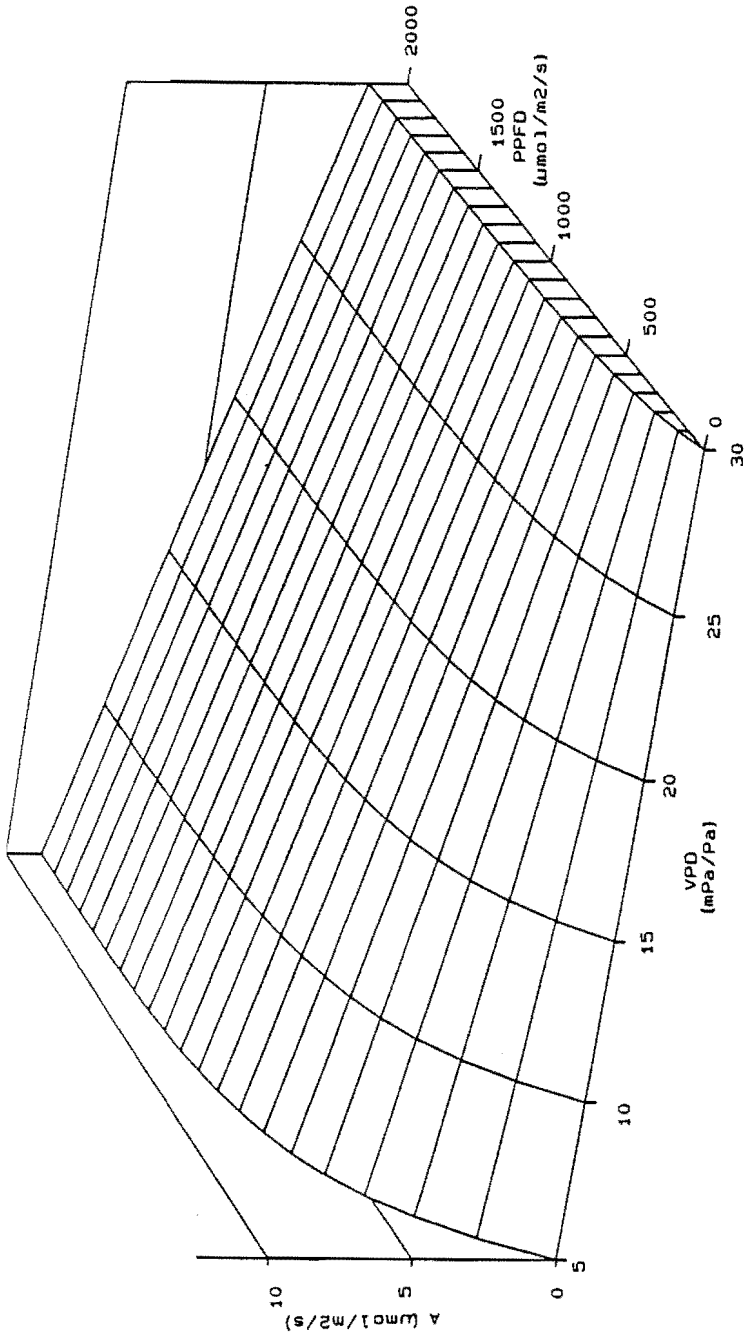

Figure 3.5 Photosynthetic response surface for PPFD and VPD.

The response surface was obtained by fitting equation 3.5 to the data shown in Fig. 3.3 using non-linear regression techniques. The equation is $A = 8.73(1 - e^{-0.003PPFD})(1 - 0.034(VPD-5.0))$ with coefficient of determination (R^2) of 0.73.

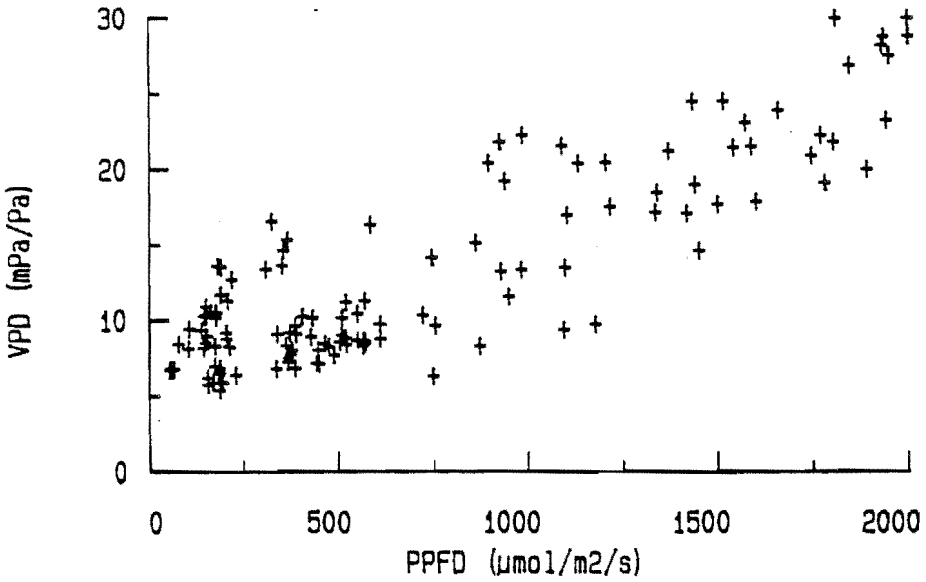

Figure 3.6 Distribution of light and VPD values from Fig. 3.3

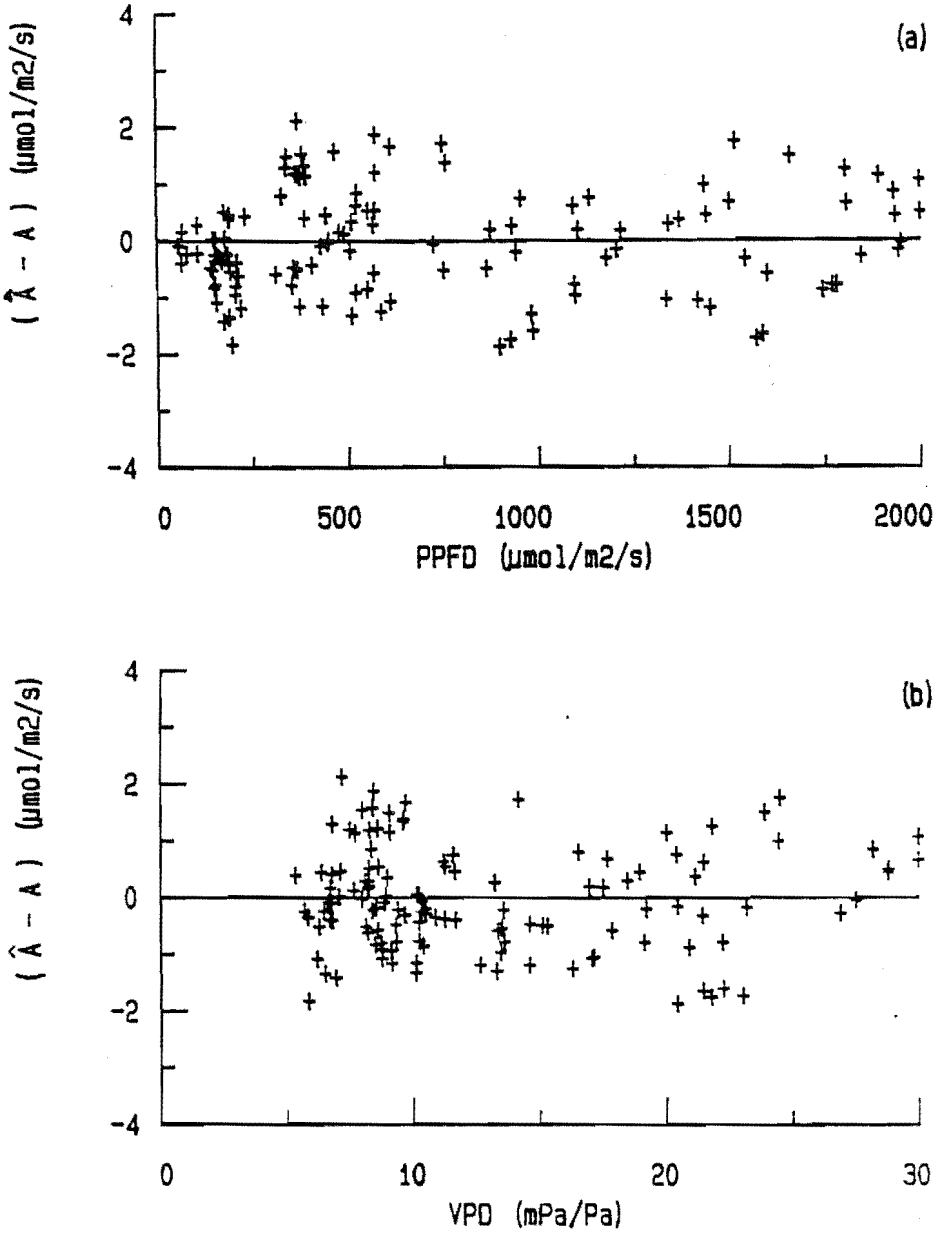

Figure 3.7 Distribution of regression residuals from Fig. 3.5.

The residuals were calculated as the difference between the observed photosynthetic rate and that computed by the model in Fig. 3.5.

(a) Related to light intensity (PPFD).

(b) Related to leaf-air vapour pressure deficit (VPD).

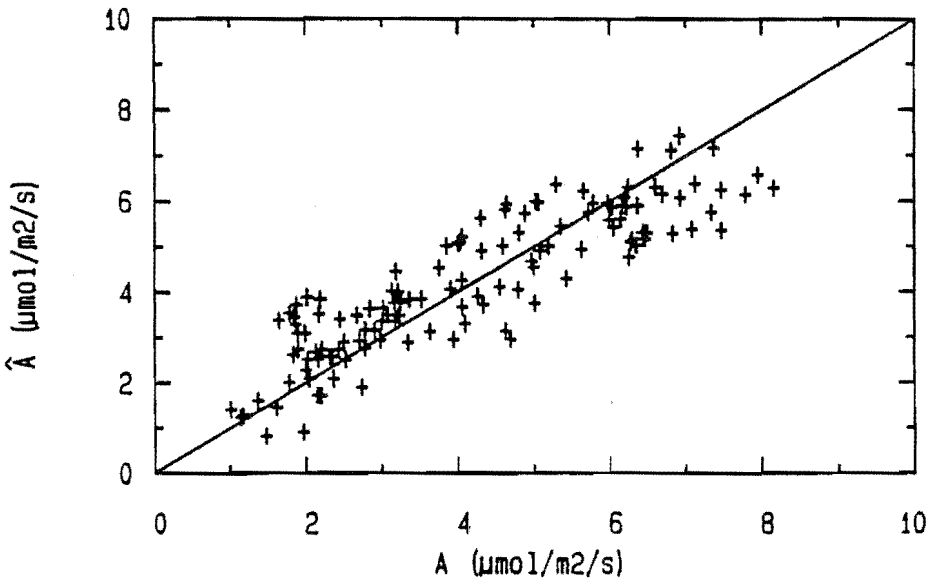

Figure 3.8 Relationship between observed photosynthetic rate and that predicted by eqn. 3.5.

The diagonal line represents an 1:1 relationship that would be expected if the modelled response is appropriate for the data.

Figure 3.5 shows a typical response surface obtained using equation 3.5 to model the effects of light and VPD on the assimilation rate of *N. fusca* saplings. The distribution of data is not ideal with light intensity being positively correlated with VPD (Fig. 3.6). The plot of residuals against light and VPD (Fig 3.7) show a relatively good fit of model to the data as does the plot of predicted against measured photosynthetic rate (Fig 3.8). The model for stomatal response to light and VPD (eqn. 3.6) gave similar results when applied to the stomatal conductance data. The models also gave a good fit with data collected from *N. menziesii* saplings. In chapter 7 data were collected under light saturated conditions and the equations were modified by removing the light sub-model.

In conclusion the equations proposed to model stomatal and photosynthetic response to VPD and light (eqns. 3.5 & 3.6) give a good fit with field data even though the distribution of the data is not ideal. The high coefficient of determination and satisfactory distribution of residuals means that the models can be used to describe variation in field data. The non-linear least squares procedure used to fit the model estimates the value and standard error of each parameter. These estimates can be used to compare between species and to investigate seasonal effects, but comparisons should be conservative with the knowledge that estimates will be biased due to the distribution of the data.

4. THE STUDY SITES.

4.1 GENERAL.

Two locations in the South Island of New Zealand were used for the field work in this study (Fig. 4.1). The Forest Research Institute nursery at Rangiora on the east coast, and the Station Creek experimental area 16 km north of Springs Junction, west of the main alpine divide (Fig. 4.2). The field work was conducted over two growing seasons between September 1984 and August 1986.

4.1.1 Rangiora.

The Forest Research Institute nursery at Rangiora, 23km north of Christchurch is the site of a *Nothofagus* provenance trial (Wilcox and Ledgard 1983) and was used to obtain reference gas exchange data in this study (Chapter 6). Mean air temperature (Fig. 4.3a) is highest in January (16.4°C) and lowest during July (5.6°C). Mean annual rainfall is 697mm (Table 4.1) which is relatively evenly distributed throughout the year (Fig. 4.3b), but drought conditions may occur during summer. The soil type at Rangiora classified as Wakanui (Yellow-grey earth of terrace land, dry-dry hygrous, New Zealand Soil Bureau (1968)).

4.1.2 Station Creek.

The Station Creek region is in an area zoned for *Nothofagus* management on the east bank of the Maruia River 16 km north of Springs Junction (Fig. 4.2) just west of the main alpine divide (Map reference NZMS S39 675180). The study sites are on a flat river terrace adjacent to Coal Creek at an altitude of 400 m and on an Ahaura soil (Yellow-brown earth of terrace land, hygrous, New Zealand Soil Bureau (1968)). The forest on the valley floor is dominated by large *N. fusca* with scattered smaller *N. menziesii*. At higher altitudes and on mid and upper slopes *N. menziesii* becomes dominant with scattered *N. fusca* and Podocarp species. Approximately half of the area was logged during trials since the early 1970's. Two sites were selected, an open site in the middle of a logged area, and an area of natural forest 250m to the west which included a recent small canopy gap. The sites were selected so that environmental parameters could be compared between the sub-canopy environment, and an exposed open area. The sites were also used for gas exchange studies with *N. fusca* and *N. menziesii* seedlings between December 1984 and May 1986. The canopy gap was created when two large *N. menziesii* trees fell over during early 1984 and had a projected area of 67m^2. The understorey of *Coprosma foetidissima* and *Nothofagus* saplings was removed beneath the canopy gap to increase the amount of light reaching the ground and any suppressed *Nothofagus* seedlings.

There are no permanent meteorological records for Station Creek, the closest permanent site being Springs Junction. Mean total rainfall at Springs Junction is 2170 mm (Table 4.1) and rainfall is unevenly distributed throughout the year (Fig. 4.3b) with a dryer period during summer and early autumn (December to March).

	Rangiora	Springs Junction
Latitude	43° 19'S	42° 20'S
Longitude	172° 34'E	172° 11'E
Map Reference (NZMS series 1)	S76 951832	S46 614020
Period for long term measurements	1965-80	1977-80
Rainfall		
Mean	697mm	2170mm
July 1984-June 1985	495mm	2374mm
July 1985-June 1986	811mm	2172mm
Air temperature		
Mean	11.3°C	9.5°C
July 1984-June 1985	12.0°C	10.1°C
July 1985-June 1986	11.8°C	Incomplete record
Distance to study site	Adjacent	16km to north.

Table 4.1 Summary of long term climate data for Springs Junction and Rangiora.

Data were collated from summaries published by the New Zealand Meteorological service (New Zealand Meteorological Service 1983, 1984-6). The data from Springs Junction were used since there are no permanent records for the Station Creek area.

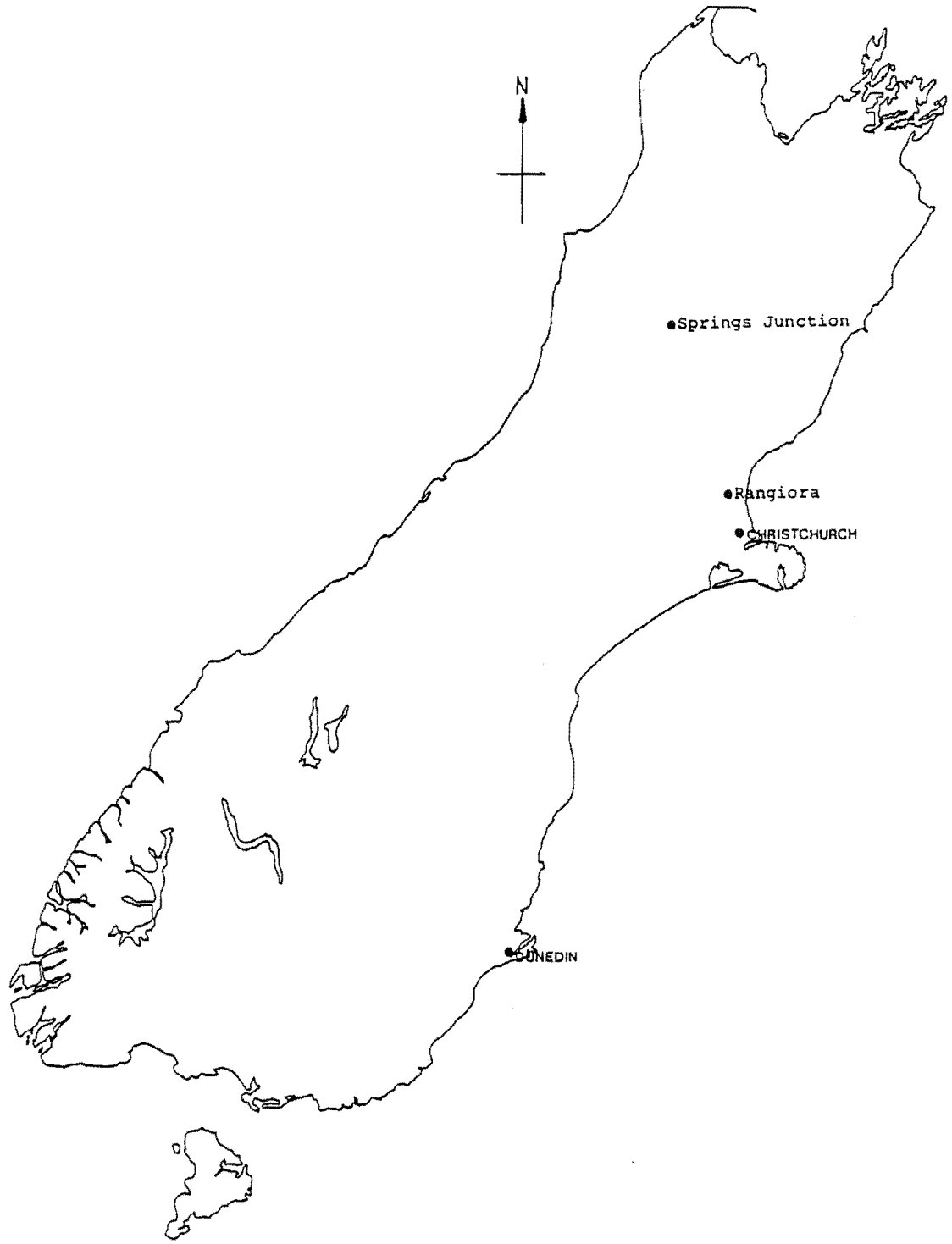

Figure 4.1 Map of the South Island, New Zealand.

The map shows the general location of the field sites used in the study. The Station Creek experimental area is 16km north of Springs Junction.

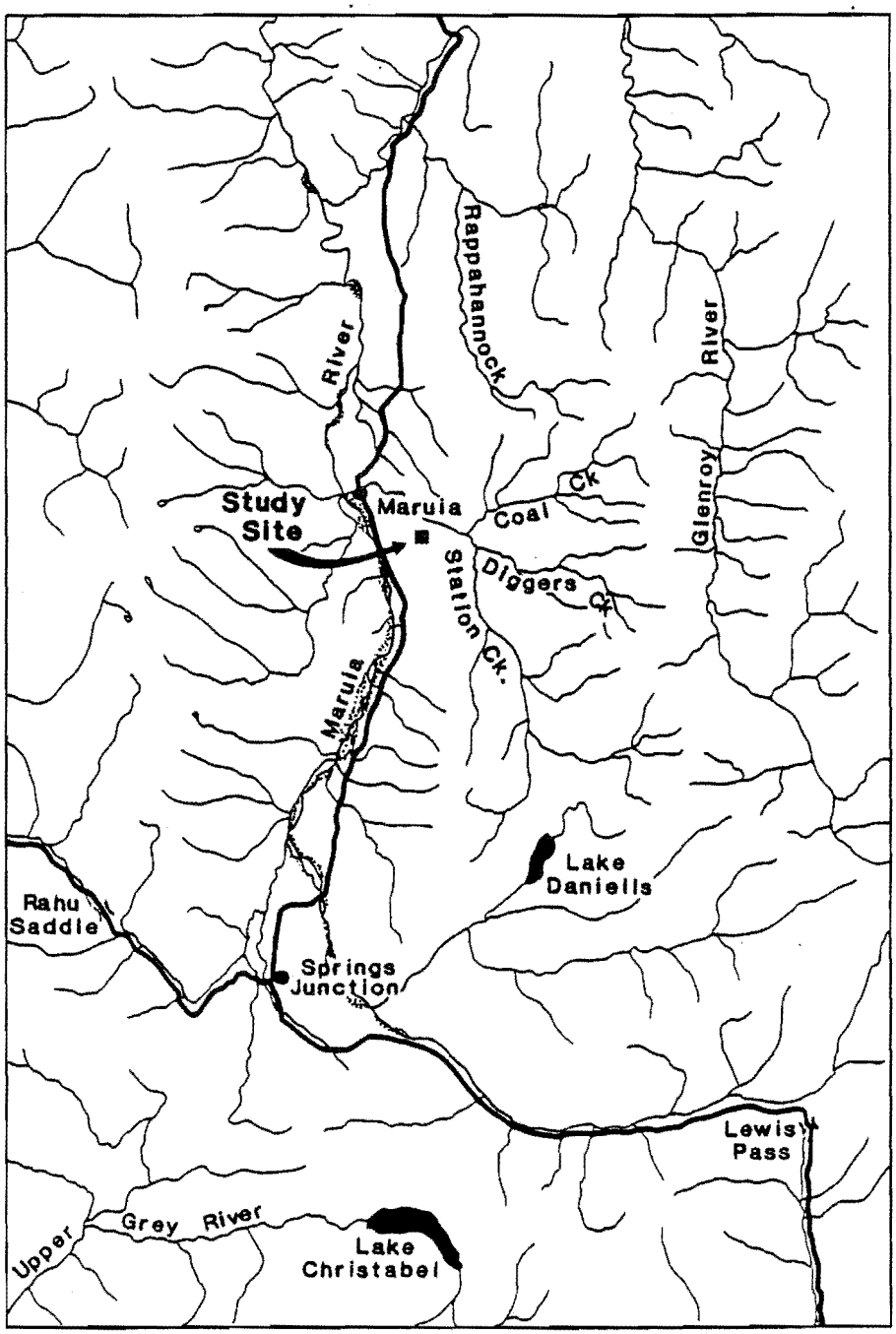

Figure 4.2 Map of the upper Maruia Valley.

The main study area at Station Creek is marked (arrow). Permanent climate data were obtained from the meteorological station sited at Springs Junction.

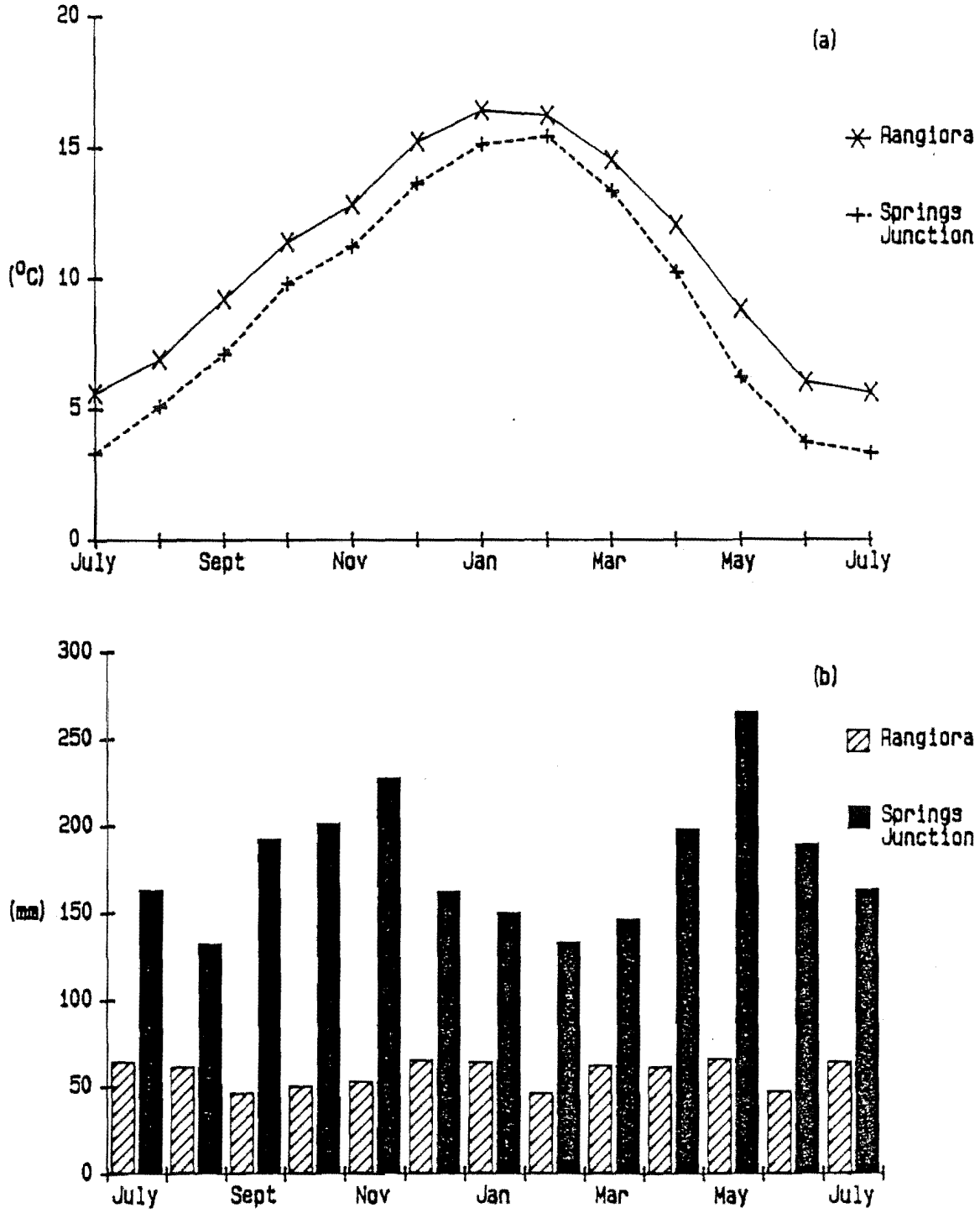

Figure 4.3 Mean monthly rainfall and air temperature at Rangiora and Springs Junction.

Data were obtained from summaries published by the New Zealand Meteorological service (New Zealand Meteorological Service 1983, 1984-6). The values for Springs Junction are the mean of data collected between 1965 and 1980 and for Rangiora between 1977 and 1980.

(a) Monthly mean of daily minimum and maximum air temperatures.

(b) Mean monthly total rainfall.

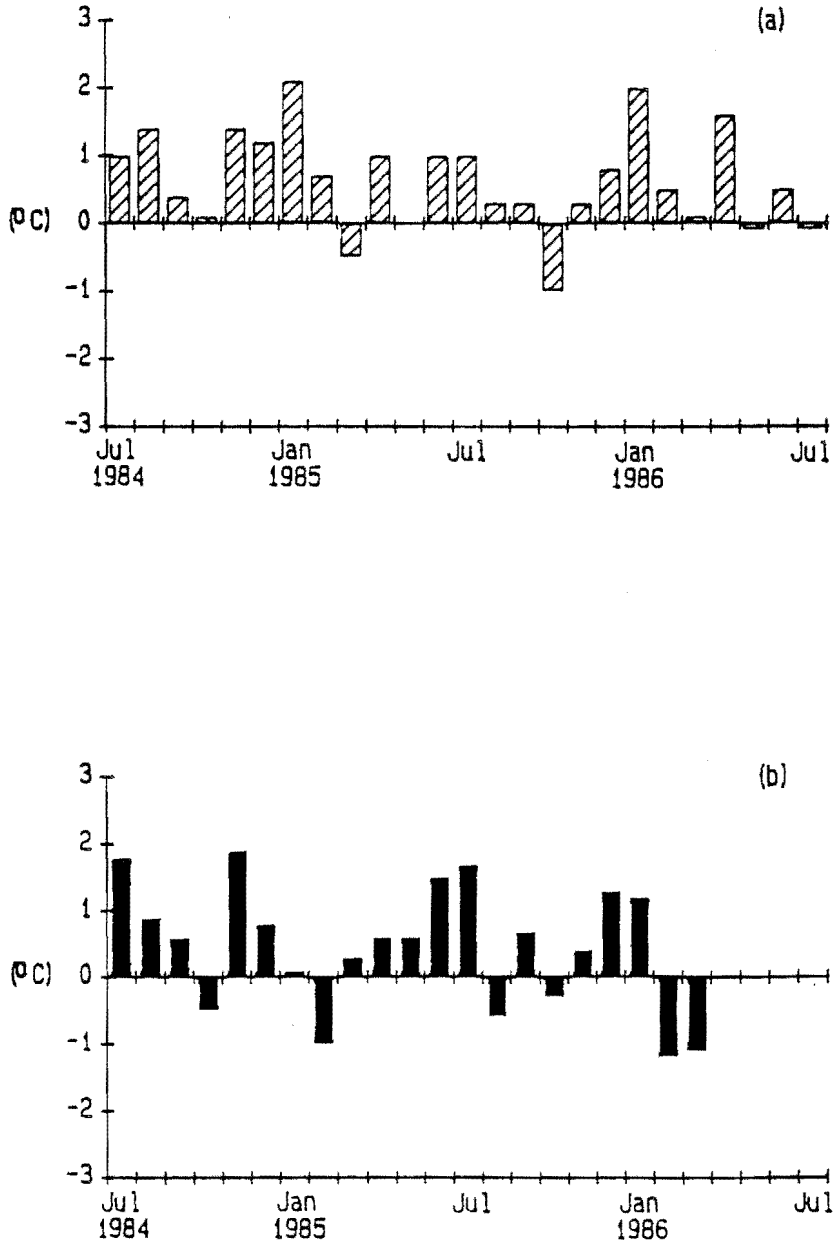

Figure 4.4 Deviations from mean monthly air temperature at Rangiora and Springs Junction between July 1984 and July 1986.

Long term mean temperatures are shown in Fig. 4.3a

(a) Rangiora.

(b) Springs Junction. (No record from April 1986).

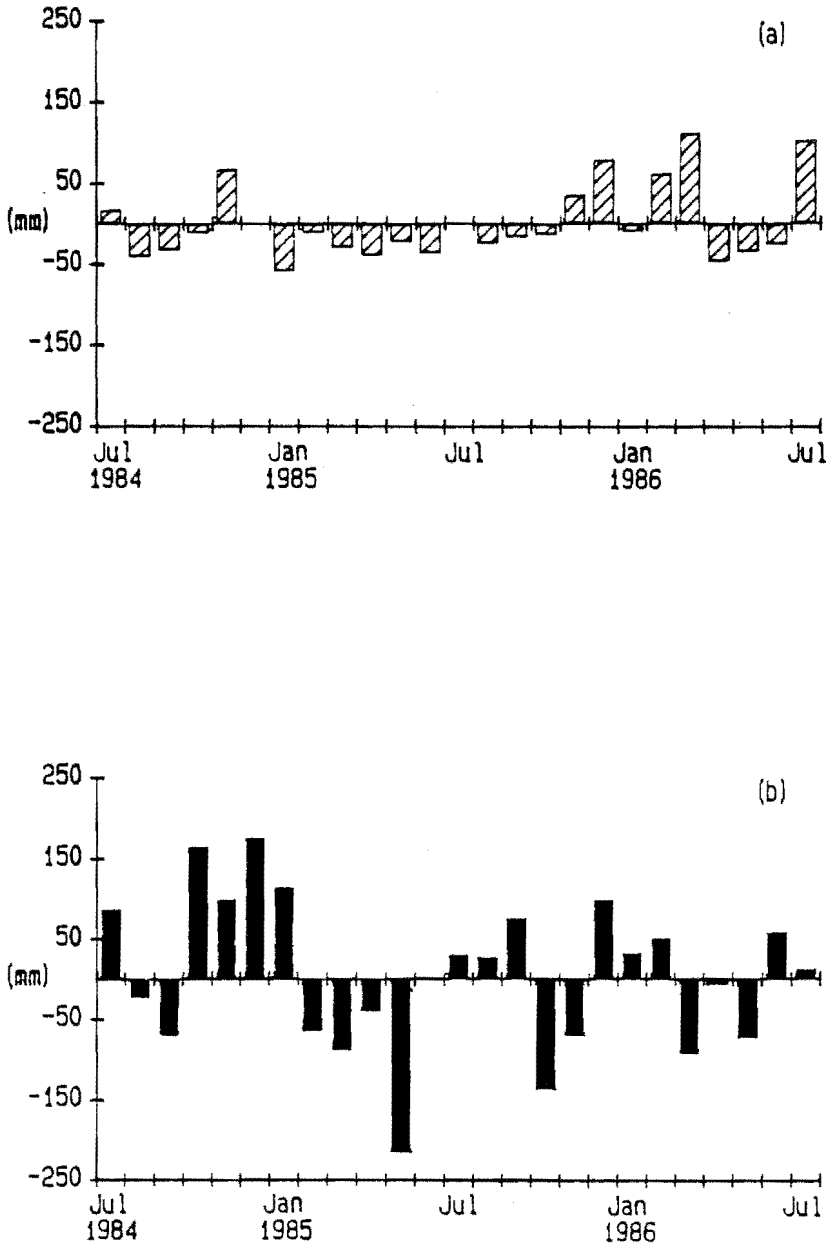

Figure 4.5 Deviations from mean monthly rainfall at Rangiora and Springs Junction between July 1984 and July 1986.

Long term rainfall data are shown in Fig. 4.3b

(a) Rangiora.

(b) Springs Junction.

4.2 CLIMATE.

Meteorological records from permanent stations at Rangiora and Springs Junction have been used to describe the regional climate during the period from July 1984 to July 1986. Air temperatures at the two sites were warmer than average during both growing seasons (Table 4.1, Fig. 4.4). There were only four months with below average temperatures at Rangiora and six at Springs Junction. Rainfall at Rangiora during the 1984–85 growing season was 29% less than average and 16% higher during the 1985–6 season (Table 4.1). During the period between July 1984 and November 1985 monthly rainfall values were mostly lower than average. This dry period was followed by a relatively moist summer. Annual rainfall at Springs Junction was similar to the long term mean for both seasons (Table 4.1). During the 1984–85 season the period between October and January (spring to summer) was wetter than usual and followed by a particularly dry period (Fig 4.5b). Rainfall during May 1985 was 80% lower than normal.

4.3 ENVIRONMENTAL DATA (STATION CREEK).

4.3.1 Methods.

At Station Creek in both the sub-canopy and open sites air and soil temperature, relative humidity and light intensity were recorded continuously between April 1985 and August 1986. Rainfall and grass temperature were recorded only on the open logged site.

Temperature. The air temperature at both sites was measured 1 m above the ground with a shielded temperature probe. Temperature was recorded at ground level by a thermohygrograph sited in a Stevenson screen. The soil temperature at a depth of 2 cm was recorded under the fully closed canopy in the center of the canopy gap and on the open site. An additional temperature probe was placed in a clump of grass on the logged site to give an unshielded temperature reading. Mean daily temperatures were calculated from the daily minimum and maximum as transcribed from monthly charts.

Relative Humidity. The relative humidity (RH) of the air at ground level was recorded under the canopy gap and on the open site by Belfort thermohygrographs. The daily minimum RH and maximum temperature at ground level were used to calculate the daily maximum atmospheric water vapour pressure deficit (VPD) as defined in equation 4.1.

$$VPD = \frac{(100 - RH)\, e_a}{100} \qquad \text{(eqn. 4.1)}$$

where:– e_a is the saturation vapour pressure of water at the ambient air temperature. Millibar units were used so that the values were of the same magnitude as estimates of leaf-air vapour pressure deficit obtained in the gas exchange measurements. (1 mbar $\approx$ 1 mPa Pa^{-1})

Rainfall. Rainfall was recorded continuously by a Belfort high-capacity recording rain gauge. Daily rainfall measurements were transcribed from monthly charts.

Light. Total daily photosynthetic photon flux density (PPFD) was recorded on the open logged site by a LI-COR LI-510 integrating light meter.

Light flux under the canopy was recorded at monthly intervals between April 1985 and April 1986, using chemical light meters as described by Young and Whitehead (1981) and Turton (1982). The chemical light meter utilizes the bleaching response of ammonium diazo paper when exposed to light. A three cm^2 booklet containing 15 layers of ammonium diazo paper were placed in a light proof petrie dish under a two cm diameter shutter. The light meters were exposed by removing the self-adhesive shutter. The paper was developed by suspension for fifteen minutes over a concentrated ammonia solution. Fully exposed paper is white or grey with unexposed paper purple. The sensitivity of the method was improved by using a reflectometer to measure partially exposed pages (Turton 1982). The number of exposed pages in each light meter is proportional to the logarithm of the total received light flux. The chemical light meters were calibrated for PPFD by placing twelve chemical light sensors next to the integrating light meter on the open site for periods ranging between two and six days. A linear regression equation was used to relate the number of exposed pages in each booklet to the logarithm of total PPFD. Separate calibrations were conducted each month, with the regression equation used to estimate PPFD values for sensors under the canopy.

The chemical light meters were placed on wooden platforms one meter above the ground on three transects across the canopy gap. Each transect started under closed canopy, passed across the canopy gap to finish under closed canopy. One transect was placed in a north/south direction with the other two running east/west. Platforms were placed at five meter intervals along each transect with two light meters per platform. The positions of the light meters are shown in figure 4.11.

4.3.2 Results

Air temperature. Mean air temperatures were similar throughout the year for the probes sited under the canopy gap and on the open logged site (Fig. 4.6a). The highest temperatures occurred in January with a monthly mean of 18.6°C on the open site and 17.4°C under the canopy gap. Minimum mean temperatures occurred during July 1986. On the open site the mean temperature was 2.3°C and under the canopy gap 2.5°C.

During most of the year the air temperature above grass (unshielded at ground level) was higher than the shielded measurements made at a height of 1m. January 1986 had the highest monthly mean temperature of 23.3°C and July 1986 the lowest of 3.8°C.

Mean daily air temperature variation (Fig. 4.6b) was lowest during winter and was lower beneath the canopy gap than on the open site throughout the year. The greatest temperature variation was observed above grass on the open site during summer. The air temperature variation at 1m above the ground on the open site was intermediate to that of the grass temperature on the open site and the air temperature beneath the canopy gap.

Soil Temperature. The soil temperature at 2cm depth (Fig 4.7a) was highest on the open site during January 1986, with a mean value for the month of 20.3°C. The mean during January under the canopy gap was 15.4°C and 15.9°C under closed canopy. Minimum mean soil temperatures occurred during July 1986 with values of 2.7°C on the open site, 3.6°C under closed canopy and 2.2°C under the canopy gap. Mean daily soil temperature variation (Fig. 4.7b) was lowest under closed canopy and highest on the open site. Differences between sites were largest during spring and autumn.

Humidity. Mean daily maximum atmospheric vapour pressure deficit (VPD) at ground level (Fig. 4.8) was higher on the open site than under the canopy gap for all months of the year. Air under the canopy gap was saturated with water vapour most of the period from April through to July 1986. On the open site, minimum VPD values of 2.5 mbar were measured in May and June 1986. Maximum mean values of 13.4 mbar on the open site and 6.1 mbar under the canopy gap were measured during November 1985.

Rainfall. Rainfall at Station Creek was slightly lower than at Springs Junction during fourteen out of sixteen months (Fig. 4.9). Total rainfall at Station Creek between July 1985 and June 1986 was 1849 mm compared with 2172 mm measured at Springs Junction for the same period.

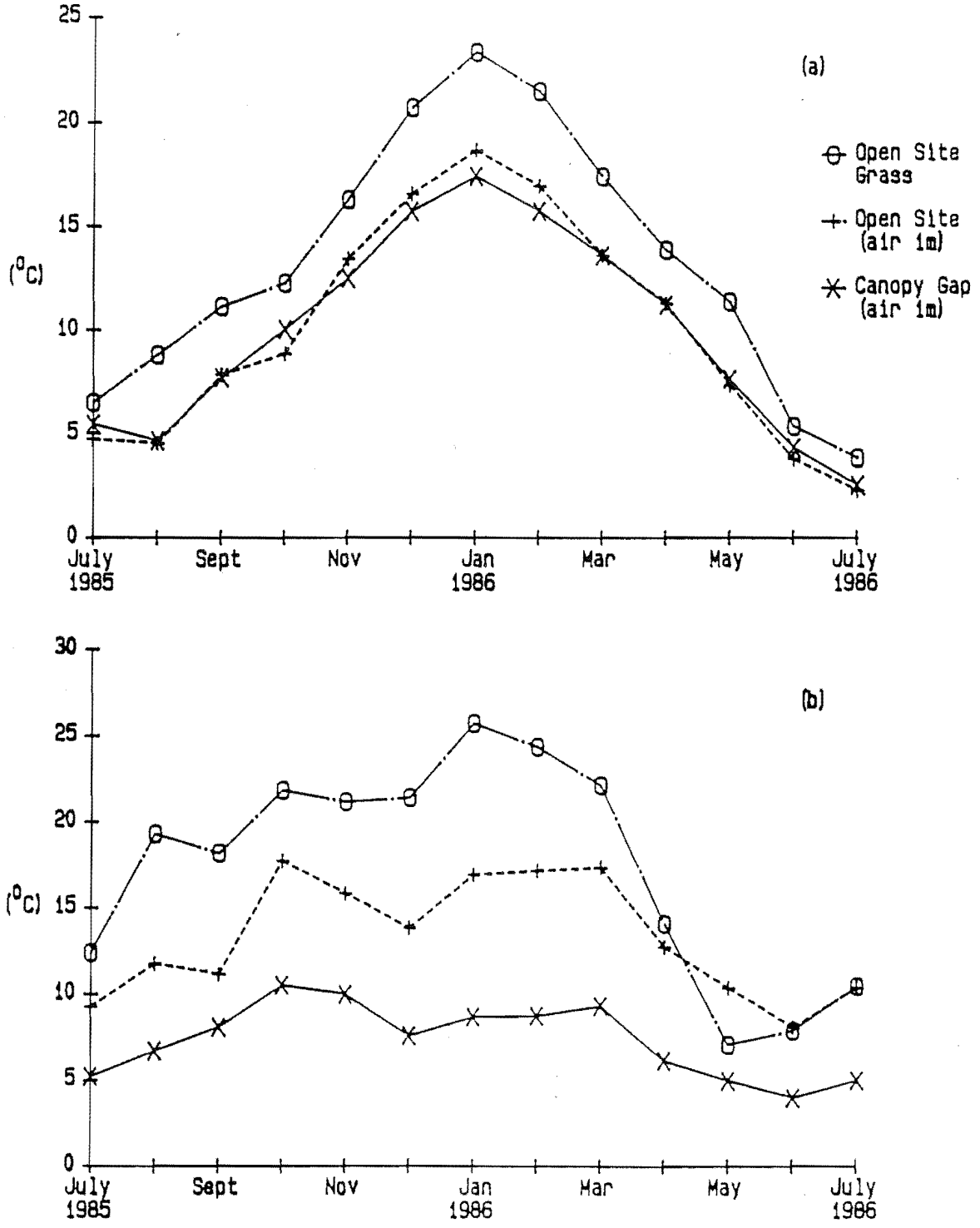

Figure 4.6 Air temperature at Station Creek.

Shielded temperature probes were placed 1m above the ground in the centre of the canopy gap and open site. An unshielded probe was placed at ground level above grass on the open site.

(a) Monthly mean of daily minimum and maximum temperature

(b) Monthly mean daily temperature variation.

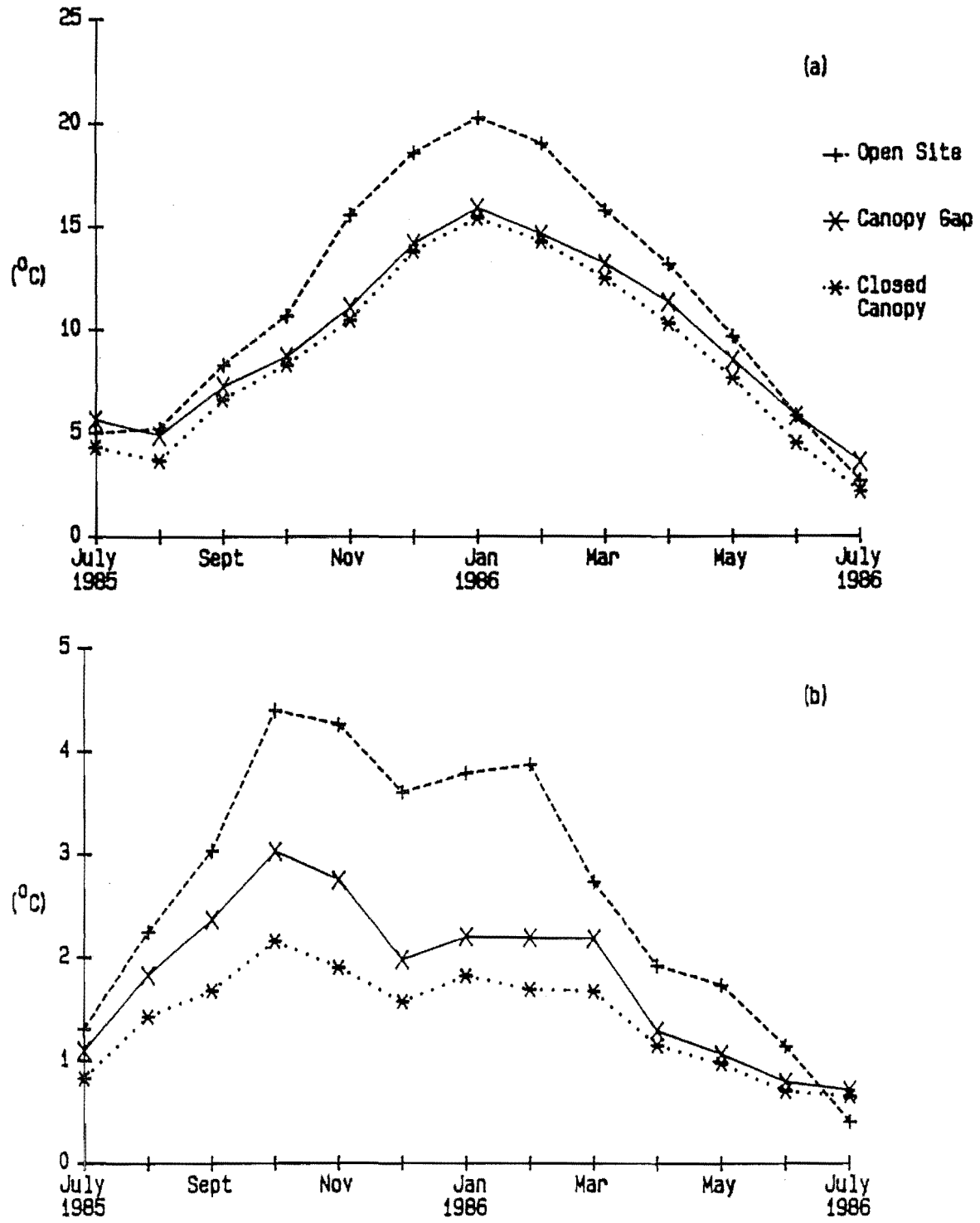

Figure 4.7 Soil temperature at Station Creek.

Temperature probes were buried at 2cm depth under closed canopy, canopy gap and on the open site.

(a) Monthly mean of daily minimum and maximum temperature

(b) Monthly mean daily temperature variation.

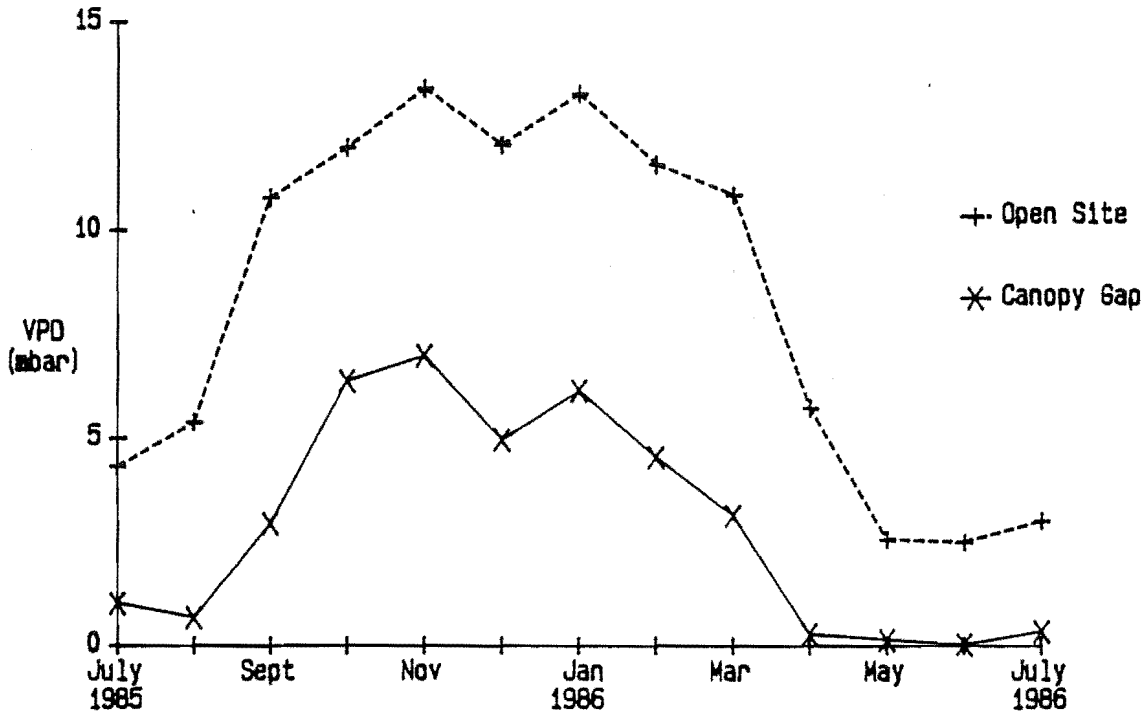

Figure 4.8 Mean daily maximum atmospheric water vapour pressure deficit (VPD) at Station Creek.

Mean daily maximum saturation vapour pressure deficit was calculated from the maximum daily temperature and minimum relative humidity.

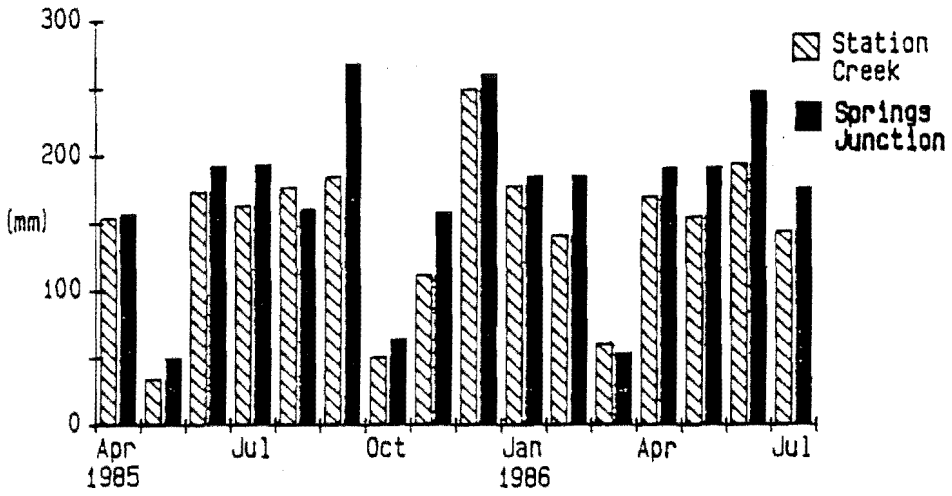

Figure 4.9 Rainfall at Station Creek and Springs Junction.

Data for Springs Junction were obtained from summaries published by the New Zealand Meteorological service (New Zealand Meteorological Service 1983, 1984-6). Data for Station Creek were obtained from a high capacity weighing rain gauge situated in the middle of a logged area.

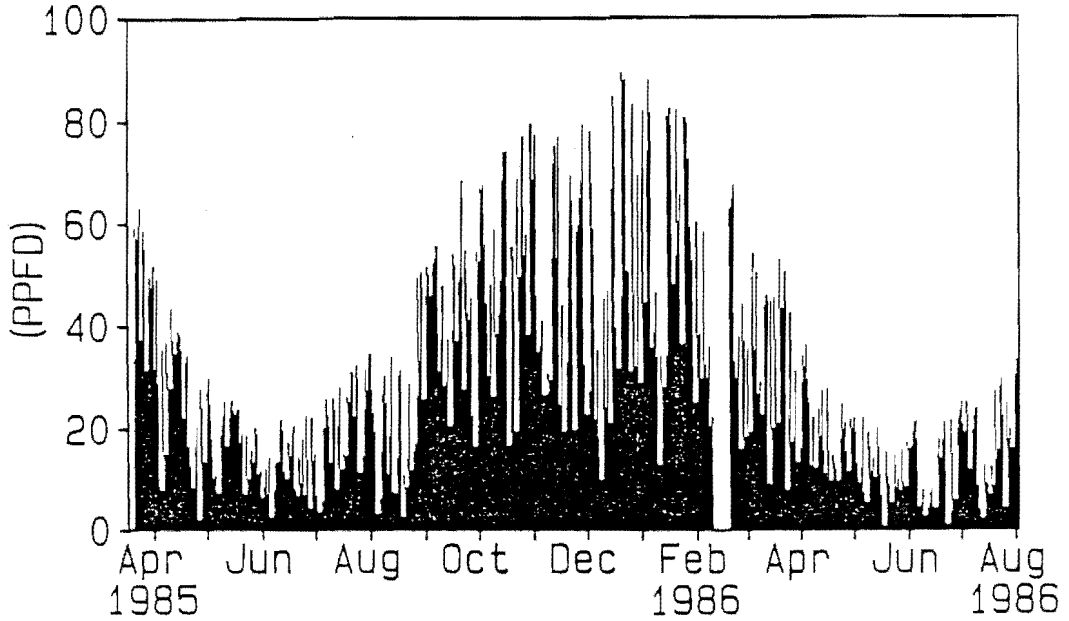

Figure 4.10 Photosynthetic Photon Flux Density (PPFD) at Station Creek.
Daily total PPFD (mol m^{-2} day^{-1}) was measured by a LI-COR LI-510 light integrator and LI-190 quantum sensor.

Light. Daily total PPFD on the open site varied between seasons and from day to day depending on weather conditions (Fig. 4.10). The maximum daily PPFD value of 89.3 moles m^{-2} s^{-1} was measured during January 1986. The lowest light values were measured during June and July, but even during summer daily totals could approach those of the winter months when dense cloud and heavy rain obscured the sun.

The positions of the chemical light meters are shown relative to the edge of the canopy gap in figure 4.11. The mean height of the canopy edge was 30m. Several chemical light meters were destroyed during the study by either excessive moisture or by animals. Figure 4.12 shows spatial and seasonal distribution of light under the canopy gap as a percentage of total PPFD measured on the open site by the light integrator. Figure 4.12a shows the mean light intensity in the center of the canopy gap over the 13 months of measurement. Figure 4.12b shows the spatial distribution along the north/south transect during winter and summer. Winter measurements were the mean of June, July and August and summer were the mean of December, January and February. Light intensities measured under the center of the canopy gap were five times higher than under closed canopy during summer but only two times higher during winter.

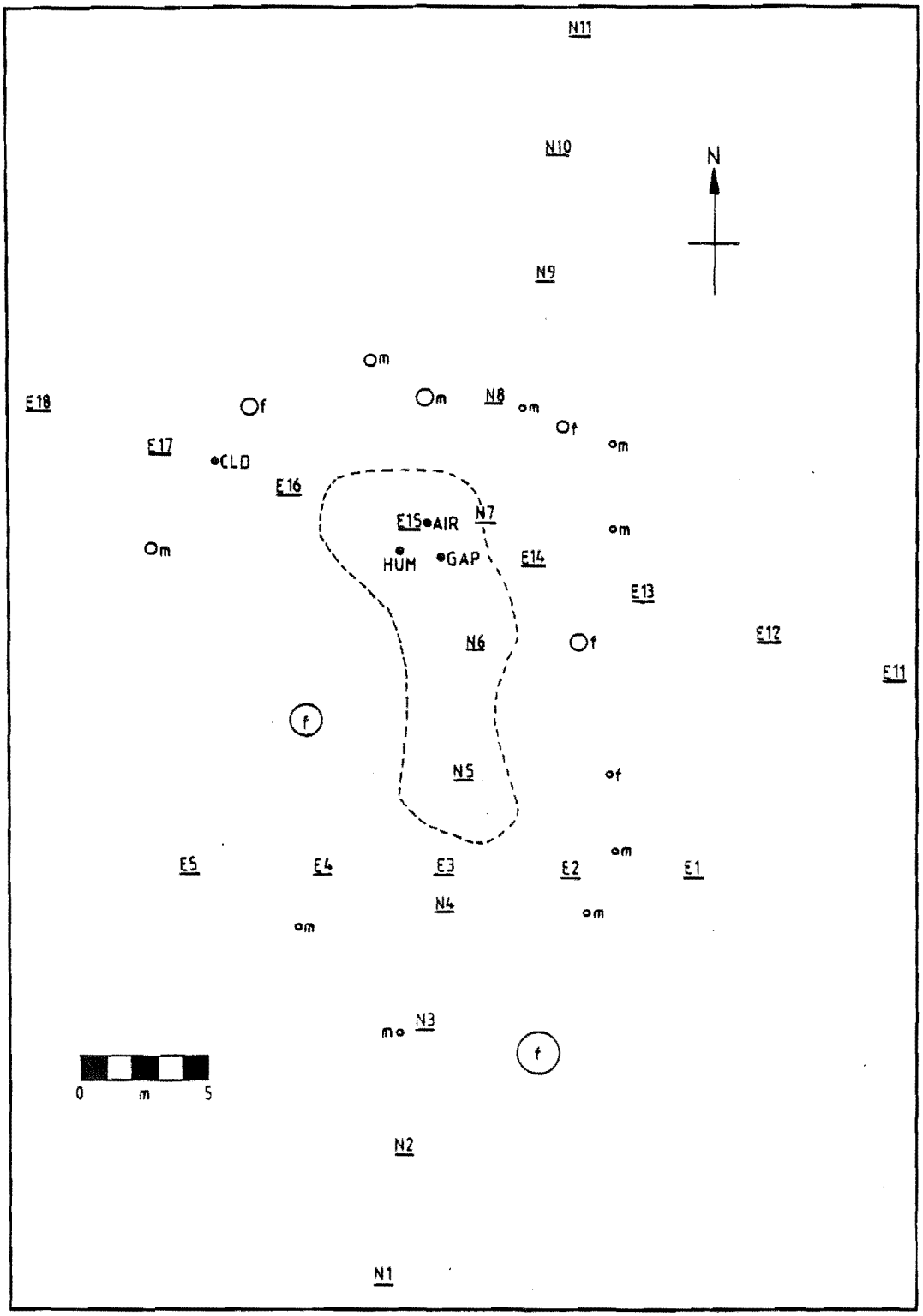

Figure 4.11 Map of the canopy gap.

Light meters were placed at 5m intervals along one north/south transect (N1..N11) and two east/west transects (E1..E5, E11..E18). The dashed line represents a projection of the canopy edge. The average height of the canopy was 30m. The circles represent the trunk diameter of the main canopy trees at a height of 1.5m (*N. menziesii* **m**, *N. fusca* **f**). The position of the air temperature probe is labelled AIR, and the two soil probes CLD (Closed canopy) and GAP (Canopy gap). The position of the thermohygrograph is marked HUM.

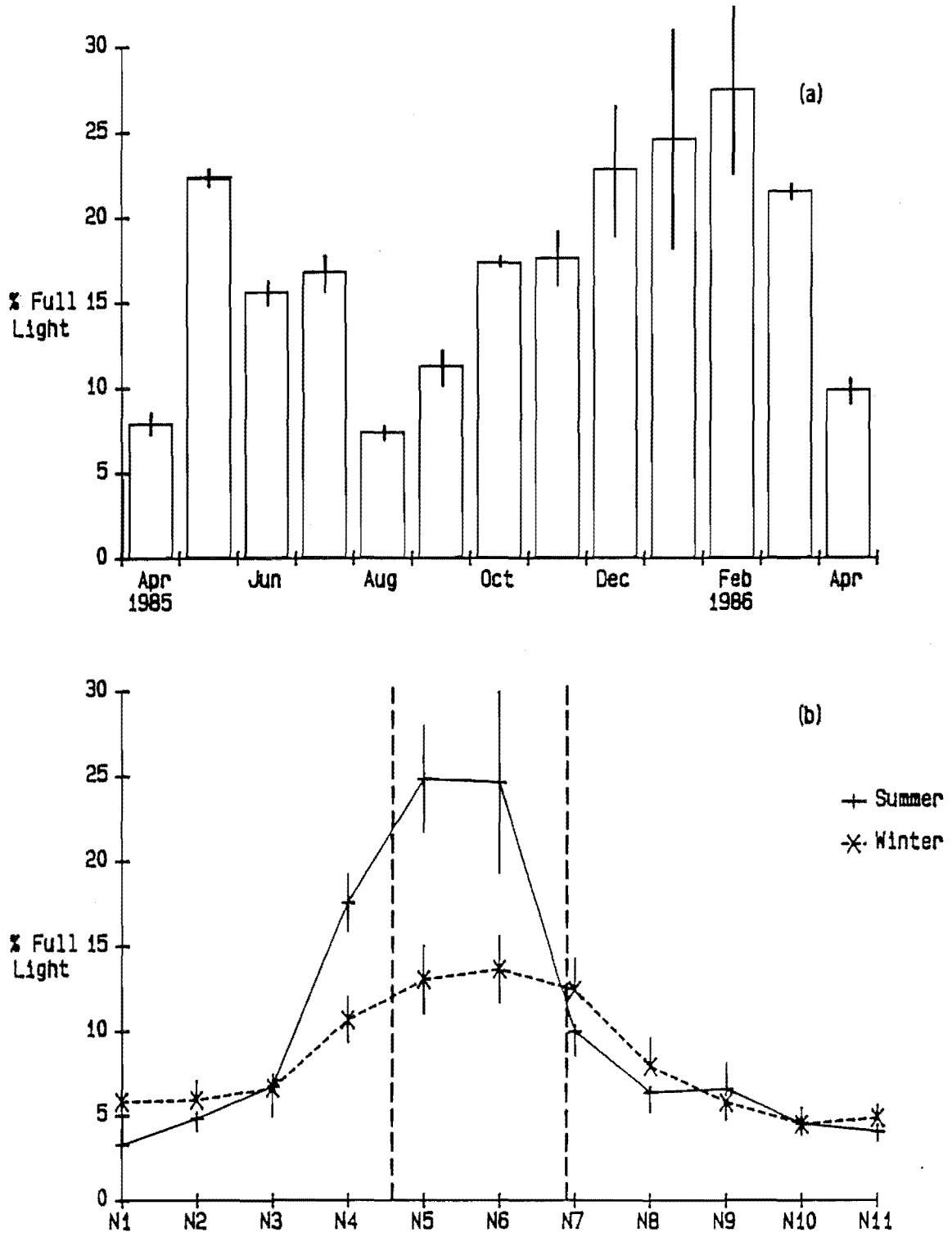

Figure 4.12 Relative light intensity beneath the canopy gap.

Total light flux was measured at a height of 1m above the ground, over a six day period using chemical light meters. Relative light intensity was calculated as the percentage of total PPFD measured on the open logged site by the LI-COR light integrator (Fig 4.9). Vertical lines represent ± 1 s.e.

(a) Seasonal variation in relative light intensity under the centre of the canopy gap. Data are the monthly mean of measurements made at positions N5 and N6 on the north transect (Fig 4.11).

(b) Spatial variation along the north transect. Data are the mean of of measurements obtained from December to February for summer and June to August for winter. The dashed lines represent the position of the canopy edge.

4.4 DISCUSSION.

4.4.1 Methods.

The amount of environmental information that could be obtained during the period of this study was limited by the availability of equipment and it's reliability. Nearly all of the equipment was affected by short-term failures usually due to clocks stopping or battery failure. A data logger would have allowed more detailed measurements and would have been more reliable. The measurement of relative humidity with a data logger under the canopy would however be difficult due to the prolonged conditions of high humidity which can damage capacitance type humidity sensors. The calculations of maximum daily VPD for both sites assumed that the highest temperature occurred at the same time as the lowest daily relative humidity measurement. The assumption is reasonable since temperature is the principle factor controlling VPD, but the estimate gives no information on the nature of daily variation.

The chemical light meters produced adequate results but tended to be damaged during periods of heavy rain which occur frequently in the Maruia Valley. The advantages of this method are that adequate replication can be obtained and that the method is inexpensive. A major disadvantage of the method is that it is difficult to obtain continuous records for remote sites because the method is labour intensive and requires continuous supervision. Another problem is that the measurements are integrated over the entire six day period, with no information on the variation during that time. The high cost of quantum sensors has made replication a problem in previous studies which utilized data loggers to characterize the sub-canopy light environment. A cheap photodiode is now available which has a response approximating that of a quantum sensor (Gutschick *et al.* 1985) and will make such studies feasible in the future. The use of data loggers in future studies could enable measurement of duration and intensity of individual sun-flecks.

4.4.2 Comparison between the Rangiora and Springs Junction regions.

Rangiora is well outside the natural range in which either *N. menziesii* or *N. fusca* are found to grow. Rainfall is considerably lower than in areas normally associated with either species. The *Nothofagus* saplings at Rangiora were growing under an artificial management regime and were irrigated at intervals throughout the season.

The Maruia valley is in a region of moderately high rainfall. The rainfall at Station Creek was lower than that measured at Springs Junction during the periods of the study. This observation is consistent with Station Creek being on the east side of the valley which tends to be drier than the west where Springs Junction is located. Rainfall also tends to decrease from south to north down the valley. The

open logged area at Station Creek, whilst having been created by artificial disturbance is quite similar to areas that occur after a large windfall. The closed canopy and canopy gap environments were sited under natural forest and had experienced minimal artificial disturbance. These two sites used in the study can be considered to represent typical sub-canopy environments in the Station Creek area.

4.4.3 Comparison of sub-canopy and open environments.

The environment under the forest canopy was very different from that where the forest had been removed. Light flux under closed canopy was 5% of that measured on the open site. Beneath the canopy gap, light flux was 10% of the open site during winter and 25% during summer. The seasonal differences are mainly due to changes in the sun's attitude relative to the edge of the canopy gap. During summer the sun's position results in a higher direct radiative flux than in winter. The lower attitude of the sun and generally cloudy conditions in winter resulted in a higher diffuse component of the total light flux. Turton (1982) found relative light intensities of between 1 and 5 % under a closed canopy of *N solandri* var. *solandri* and (McCracken *pers comm.*) found values of between 5 and 10 % under a canopy of *N. truncata*. PPFD measured under closed canopy at Station Creek in the current study was 5% of the flux measured on the open site.

The general trends in PPFD from closed canopy through to canopy gap and open site can be used to make qualitative inferences about energy flux in the forest. The presence of forest modifies the energy flux of a site. Total flux on an open site depends on the season and weather patterns. On the forest floor, under either closed canopy or a canopy gap, flux will depend on the density of foliage in the path of the radiation. The flux under a canopy gap will be intermediate to that on an open site or under fully closed canopy. The difference between closed canopy and a canopy gap is determined by the size of the gap, and the height of the edge of the canopy. Small gaps will have energy fluxes similar to closed canopy whilst larger gaps will be similar to an open site. The differences in energy flux between sites will be important for plant growth through effects on temperature, water relations and photosynthesis.

Mean air temperatures on the open site and under the canopy gap were similar for most of the year. During summer mean temperature was slightly higher on the open site. Mean daily temperature variation was considerably higher on the open site than under the canopy gap throughout the year. Variation was greatest during summer with a marked decrease in December 1985 (Fig. 4.6b) correlating with the wet cloudy conditions during that month. The variation is more easily explained by the energy flux at each site. The open site had higher energy flux and therefore a greater daily variation in energy and hence temperature. The unshielded temperature probe placed above grass on the open site measured both higher mean temperatures and daily variation. This result is typical of surface temperature

measurements demonstrating the extremes of temperature which may occur at the ground surface. During summer on occasions temperatures of up to 45°C were recorded and grass frosts of -12°C were recorded during winter.

Soil temperature is often considered to be a useful integrator of temperature for a site. Mean soil temperatures under both closed canopy and canopy gap were similar for most of the year. Mean daily temperature variation was higher under the canopy gap due to the greater energy flux. Soil temperature variation like the air temperature showed a decrease during December 1985 due to the weather conditions. Soil temperature on the open site was higher than under the canopy for most of the year. Temperature variation was highest on the open site reflecting the energy flux of the site.

Atmospheric water vapour pressure deficit (VPD) is determined by temperature and relative humidity. The higher temperatures observed on the open site resulted in higher VPD measurements throughout the year. Under the canopy gap the lower temperatures resulted in lower VPD values. Under the canopy gap and closed canopy transpiration by the trees and understorey is important in maintaining a high relative humidity. The low wind conditions under the canopy reduce air mixing which also maintains high humidity. The reduced energy flux under closed canopy and canopy gap lowers the evaporative water loss compared to the open site. On the open site during summer the dry conditions and high surface temperatures combined to dry the upper layers of the soil.

5. RANGIORA GAS EXCHANGE MEASUREMENTS.

5.1 INTRODUCTION.

The Rangiora nursery of the Forest Research Institute was the site of a *Nothofagus* provenance trial which was planted out in 1980 (Wilcox and Ledgard 1983). At the start of the current study the saplings were 4 years old and many were in excess of two meters tall. The trial presented an excellent opportunity to obtain reference data needed to compare the rates of gas exchange of the sun foliage of rapidly growing *N. fusca* and *N. menziesii* saplings. There were four objectives for the gas exchange measurements at Rangiora.

1. To obtain estimates of the maximum photosynthetic rates and stomatal conductance of *N. fusca* and *N. menziesii* for comparison with that of other *Nothofagus* species previously published.

2. To compare the gas exchange characteristics of *N. fusca* and *N. menziesii* growing in the open at Rangiora and Station Creek (Chapter 6) and to relate any differences to the environmental characteristics as described in chapter 4.

3. To obtain estimates of stomatal and photosynthetic sensitivity to VPD for sun foliage of *N. fusca* and *N. menziesii* for comparison with sun and shade foliage growing at Station Creek (Chapters 6 and 7).

4. To investigate the nature of seasonal variation in gas exchange parameters.

5.2 METHODS.

5.2.1 The Provenance trial.

The provenance trial at Rangiora was described by Wilcox and Ledgard (1983). The seed was collected by New Zealand Forest Service employees during 1979 between late February and early May. The seed was stratified for eight weeks under moist conditions at 4°C and sown into seed boxes in October 1979. In January 1980 the seedlings were lined out into replicated experimental plots in a randomized block design. Initially between 10 and 25 seedlings were planted per provenance in each of five blocks. The number of individuals which survived from the initial planting in the nursery was reduced by death and thinning and many provenances were not well represented in the trial at the start of the current project (Spring 1984). For this reason two or three well replicated provenances were selected from the extreme north and south of the distributions of *N. fusca* and *N. menziesii*. The *N. fusca* provenance selected were Moanui near Rotorua (Long. 38° 25', Lat.177° 25', Alt. 600m) and Eglington valley in Southland (Long. 45° 06'' Lat. 167° 57'Alt. 290m). For *N. menziesii* the provenances were Mt. Te Aroha in Auckland (Long. 37° 32', Lat. 175° 45', Alt.930m) and two in

Southland, Rowallan (Long. 46° 01', Lat. 167° 36', Alt. 220m) and the Catlins (Long. 46° 01', Lat. 169° 27', Alt.300m). It was believed that selecting provenances from the extremes of the distributions would be most likely to identify provenance or ecotype differences within each species.

5.2.2 Gas Exchange Measurements.

Gas exchange measurements were made using a LI-COR LI-6000 portable photosynthesis system as described in chapter 2. At intervals throughout the period from November 1984 to January 1986 a series of measurements were obtained on sun foliage of *N. fusca* and *N. menziesii*. Current seasons foliage was selected and any diseased or damaged foliage was removed by cutting. The twig was then tagged and placed in the chamber which was held horizontally by a tripod. A series of five 'pages' of data were recorded by the LI-6000 for each twig before selecting the next sample. The logging intervals and air flow rate through the system were varied to maintain chamber relative humidity constant and obtain a CO_2 depletion of between 15 and 30 μmol mol^{-1} for each page. The actual values selected depended on foliage type, season and weather conditions. The environmental conditions in the chamber were determined by the ambient conditions at the start of each 'page'. The CO_2 analyzer zero point was adjusted between each sample and the analyzer shielded from direct radiation to reduce temperature effects on zero and span shift. The analyzer span was calibrated every one to two hours using a reference gas of approximately 800 μmol mol^{-1} CO_2 in air.

The series of measurements commenced in the morning as soon as the foliage was dry and continued during the day until either dew formed on the foliage or the LI-6000's memory was full. The foliage was removed by cutting at the end of each series of measurements and placed in cold storage until the foliage area and weight could be determined. Leaf area was measured using a Delta-T leaf area meter (Delta-T Devices, 128 Low Road, Burwell, Cambridge.) and then the foliage was dried at 70°C before weighing.

Gas exchange measurements were not conducted when it was raining or extremely windy to prevent damage to the equipment. During periods of rapidly fluctuating light intensity due to partial cloud cover and wind, the gas exchange estimates were extremely variable due to the frequent changes in the ambient environment, and hence such data were removed from the analysis. When the weather permitted several consecutive days measurement would be obtained each month, however much of the period between November 1985 and January 1986 was considerably wetter than normal (Chapter 4) and the number of days potentially available for gas exchange were limited. The LI-6000 was returned to LI-COR for upgrading during the winter of 1985 and hence no measurements could be made during this period.

5.2.3 Data Analysis.

The data from the gas exchange measurements were analyzed using the models developed in chapter 3. The models were used to obtain estimates of the maximum rates of photosynthesis and stomatal conductance, and their sensitivity to VPD. The curvature of the light response of stomatal conductance and photosynthesis is an indication of the initial slope of the light response curve. The light saturation point was determined from the curvature constant, and was defined as the light intensity at which photosynthesis or stomatal conductance was 90% of its maximum value. No significant differences could be determined between provenances within each species and hence data for each provenance were pooled within a species.

5.2.4 Xylem Water Potential.

The equilibrium water status of the sapling was determined by measuring the 'Pre-Dawn' water potentials of the saplings with a pressure bomb (Scholander *et al.* 1965) on a limited number of occasions during the period of gas exchange measurements.

5.3 RESULTS.

Estimates of A_{max} for *N. menziesii* were consistently higher than those for *N. fusca* (Table 5.1). Both species showed a seasonal decrease in the A_{max} from a maximum observed with new foliage in spring and early summer. The highest photosynthetic rates were measured during the early summer of the 1985-86 season. The relationship between the estimates of A_{max} and g_{max} (Fig. 5.1) shows that these estimates are positively correlated and hence the estimates for g_{max} follow the same patterns as for A_{max}. The curve fitting procedure failed to converge with the stomatal conductance data for both species from January 1985 as well as in May 1985 for *N. fusca*.

The stomatal sensitivity to VPD (Table 5.2) was similar in both species, but the estimates were quite variable. The sensitivity of photosynthesis to VPD (Table 5.1) tended to be lower than that for stomatal conductance and decreased as the foliage aged.

The photosynthetic light saturation points (Table 5.1) were higher in new foliage of both species and declined as the foliage aged. The estimates obtained with data from early summer in the 1985-6 season were considerably higher than those obtained from the previous season. The light saturation points for stomatal opening (Table 5.2) were much lower than those for photosynthesis and display less seasonal variation.

The specific leaf weight (Table 5.1) of the foliage used in the gas exchange measurements was higher in *N. menziesii* and tended to increase as the foliage

aged. The pre-dawn water potential measurements (Table 5.3) were lowest during January 1985 corresponding with a particularly dry period (Chapter 4). During the following season they were much higher reflecting the particularly wet spring and summer.

N. fusca	A_{max} (μmol m^{-2} s^{-1})	Q (x1000)	Sat (μmol m^{-2} s^{-1})	D_A (%)	N	F	R^2	CV (%)	SLW (g m^{-2})
January 1985	8.73±0.43	2.97±0.28	775	3.37±0.14	127	210.5	.77	21.7	N/A
April 1985	6.42±0.29	5.10±0.41	451	1.72±0.18	150	198.7	.73	26.2	81.2±2.5
May 1985	5.59±0.46	6.37±0.10	361	2.31±1.25	55	87.2	.77	16.5	N/A
September 1985	4.20±0.17	6.90±0.69	334	0.62±0.40	219	55.6	.34	21.2	85.2±2.4
December 1985 (new foliage)	14.21±0.62	1.96±0.16	1175	1.79±0.09	138	98.6	.59	15.3	79.3±3.7

N. menziesii	A_{max} (μmol m^{-2} s^{-1})	Q (x1000)	Sat (μmol m^{-2} s^{-1})	D_A (%)	N	F	R^2	CV (%)	SLW (g m^{-2})
December 1984	12.87±0.62	2.70±0.30	853	2.07±0.20	180	111.1	.56	18.9	123.4±3.9
January 1985	8.51±0.66	3.04±0.36	757	2.12±0.19	107	57.2	.52	23.3	110.5±2.5
April 1985	9.04±0.55	3.92±0.35	587	1.84±0.18	120	260.5	.82	16.4	125.5±3.1
July 1985	6.16±0.37	9.53±2.04	242	0.78±0.73	64	48.2	.61	23.9	159.7±2.8
September 1985	7.12±0.18	4.63±0.55	497	0.93±0.12	214	25.8	.20	18.8	140.5±2.9
January 1986 (new foliage)	14.27±0.37	1.78±0.12	1294	1.58±0.65	116	238.1	.81	11.8	117.0±4.2

Table 5.1 Estimates of photosynthetic parameters for *N. fusca* and *N. menziesii* growing in the open at Rangiora.

The estimates were obtained using non-linear least squares regression techniques to fit equation 3.5 to porometry data obtained at Rangiora under ambient conditions. A_{max} is the maximum photosynthetic rate, Q the initial slope of the light response curve, Sat the 90% light saturation point, D_A the sensitivity of photosynthesis to VPD, N the number of data used, F the F ratio from the regression analysis of variance (with [2,N-3] degrees of freedom), R^2 the coefficient of determination, CV the coefficient of variation, and SLW then specific leaf weight of the foliage (N/A, sample destroyed by fungal degradation).

N. fusca	g_{max} (mmol m^{-2} s^{-1})	Q (x1000)	Sat (μmol m^{-2} s^{-1})	D_g (%)	N	F	R^2	CV (%)
January 1985		Not Converging						
April 1985	52.4±2.8	10.3±1.4	224	2.94±0.19	150	77.0	.51	38.8
May 1985		Not Converging						
September 1985	91.3±2.9	7.2±0.7	321	2.95±0.22	219	63.1	.37	23.9
December 1985 (new foliage)	160.1±6.8	4.2±0.6	537	2.27±0.09	138	99.2	.60	22.0

N. menziesii	g_{max} (mmol m^{-2} s^{-1})	Q (x1000)	Sat (μmol m^{-2} s^{-1})	D_g (%)	N	F	R^2	CV (%)
December 1984	224.0±5.7	13.2±2.0	175	2.80±0.15	180	98.0	.53	22.9
January 1985		Not Converging						
April 1985	97.6±6.5	9.3±1.6	248	3.51±0.20	120	44.2	.43	34.1
July 1985	70.0±4.1	11.9±3.0	194	5.05±0.55	64	20.0	.40	31.7
September 1985	72.2±2.1	11.1±4.3	207	0.94±0.15	214	16.0	.13	23.2
January 1986 (new foliage)	191.7±4.8	7.3±1.2	315	2.16±0.07	116	193.4	.77	17.9

Table 5.2 Estimates of stomatal parameters for *N. fusca* and *N. menziesii* growing in the open at Rangiora.

The estimates were obtained using non-linear least squares regression techniques to fit equation 3.6 to porometry data obtained at Rangiora under ambient conditions. g_{max} is the maximum stomatal conductance, and D_g is the sensitivity of stomatal conductance to VPD, other details as for Table 5.1.

Date	*N. fusca*	*N. menziesii*
17/01/1986	-0.628±0.23	-0.615±0.34
20/04/1986	-0.098±0.09	-0.090±0.07
22/09/1986	-0.113±0.09	-0.143±0.21
30/12/1986	-0.197±0.20	-0.213±0.22

Table 5.3 Pre-dawn xylem water potential measurements at Rangiora.

Xylem water potential (MPa) was measured using a pressure Bomb (Scholander *et al.* 1965) and each point is the mean of at least eight replicates.

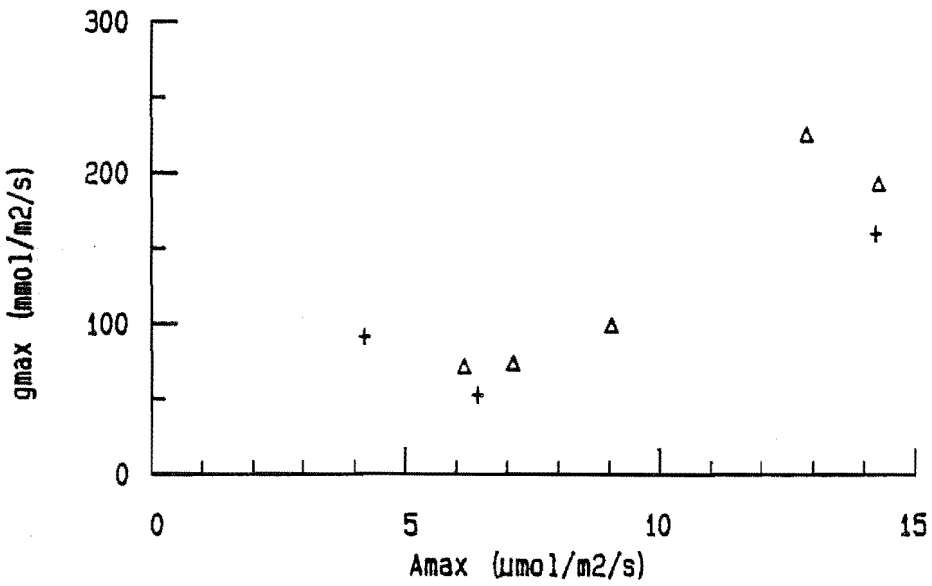

Figure 5.1 Relationship between the estimates of A_{max} and g_{max}.

The estimates for A_{max} were obtained from Table 5.1 and g_{max} from Table 5.2. (*N. menziesii* Δ, *N. fusca* +)

5.4 DISCUSSION.

The prediction that photosynthesis would be higher in foliage of *N. fusca* than *N. menziesii* has been shown to be incorrect. The prediction was based upon two assumptions, the first that *N. fusca* would have high rates of assimilation since its rates of diameter and height growth (Wilcox and Ledgard 1983) were higher. The second reason was that *N. fusca* foliage lives for a shorter period of time than *N. menziesii*, and short lived foliage tends to have high photosynthetic rates. These two assumptions need to be examined since the differences in the maximum photosynthetic rates between the species was actually the opposite to that predicted. If the rates of photosynthesis are compared on a unit weight basis the differences between the species are reduced since *N. menziesii* had a higher specific leaf weight than *N. fusca* (Table 5.1). The differences in the rates of diameter and height growth observed in the same provenance trial by Wilcox and Ledgard (1983) cannot however be explained by differences in photosynthetic rates irrespective of the way that these measurements are expressed. The differences between the species must therefore be due to the patterns of carbon allocation and relative maintenance costs in the two species.

The decline in A_{max} and g_{max} as the foliage of both species aged may in part have been due to the moderate water stress that developed in the saplings during the dry 1984–5 summer. The lowest pre-dawn water potential measurements were observed during January 1985 (Table 5.3) during a period of below average rainfall (Chapter 4) with frequent drying Nor'Westerly (Föhn) winds. Estimates of photosynthesis and stomatal conductance obtained in January 1986 during a moist summer were much higher than the previous season, indicating that water stress during the 1984–5 season had reduced the rates of gas exchange of both species.

As the foliage of both species aged, the photosynthetic and stomatal response to light and VPD declined, with both the light compensation point and sensitivity to VPD declining from a maximum in early summer. By the end of winter (September) A_{max} in *N. fusca* was only 4.2 μmol m^{-2} s^{-1} and the responses to changes in light and VPD were low. A_{max} was slightly over one third of the highest estimate of 14.2 μmol m^{-2} s^{-1} obtained in December 1985. The low A_{max} estimate in July would have also been partly due to senescence since *N. fusca* looses most of its previous season's foliage by November. *N. menziesii* was less affected by aging with the lowest A_{max} estimate of 6.2 μmol m^{-2} s^{-1} obtained in July 1985 which was just under half of the highest of 14.3 μmol m^{-2} s^{-1} obtained in January 1986. September's estimate was higher than July's indicating that *N. menziesii* foliage had some ability to recover during spring. The differences in the effects of leaf aging on the gas exchange of *N. fusca* and *N. menziesii* foliage would be expected since *N. menziesii* foliage usually lasts an additional two seasons longer than *N. fusca*.

The poor photosynthetic response to light and VPD during and after winter were reflected by low coefficients of determination (R^2 Tables 5.1 and 5.2), however the coefficients of variation (CV) were also low indicating that the amount of unexplained variation was not proportionally higher than when a good fit was obtained with new foliage. The seasonal variation in stomatal conductance was less marked but may have been masked by the inability of the curve fitting procedure to converge with data for both species from January 1985 and for *N. fusca* during May 1985. It is significant that the January 1985 data could not be modelled indicating that the stomatal responses to light and VPD were adversely affected by the water stress which occurred during that period. The long term effect of the stress on stomatal conductance was less marked than for photosynthesis.

The light saturation points for stomatal conductance estimated by the model (Table 5.2) were lower than those for photosynthesis (Table 5.1). The low light intensities at which stomatal opening was estimated to saturate indicates that under most conditions VPD was the principle factor determining stomatal conductance. The fit of the stomatal conductance model tended to be worse than for the photosynthesis model and was worst with data from September 1985. The relationship between the estimates of A_{max} and g_{max} (Fig. 5.1) was essentially a straight line which agrees with the suggestion by Wong *et al.* (1979) that there is a strong relationship between these two parameters, and provides verification for the curve fitting procedures used in this study to obtain the estimates.

The estimates of A_{max} agree with previous measurements using similar types of *Nothofagus* foliage (Read and Hill 1985, Benecke and Evans 1986). A_{max} of *N. fusca* during early summer was the same as that measure for *N. truncata* by Benecke and Evans (1986), who also observed higher A_{max} estimates during a moist summer than during a drought. The similarity in the gas exchange parameters of *N. truncata* and *N. fusca* is not surprising since the foliage morphology is similar and the species are considered to be closely related (Wardle 1984).

The estimates of stomatal and photosynthetic sensitivity to VPD are in close agreement with those of Benecke and Evans (1986). They reported the stomatal sensitivity to VPD of new *N. truncata* foliage to be 2.6% reducing to 1.6% in mature sun foliage and 0.6% in shade foliage. They also found that as the sensitivity decreased the coefficient of determination (R^2) for the regression declined from 0.9 in new foliage to 0.1 for the shade foliage.

The estimate of the light saturation point for *N. truncata* at a PPFD of 720 μmol m^{-2} s^{-1} (Benecke and Evans 1986) agrees with similar estimates obtained in this study. There have been no previous reports of the light saturation points for photosynthesis and stomatal conductance declining due to the effects of aging or drought on *Nothofagus* foliage.

The main objective of using the model was to obtain estimates of A_{max}, g_{max} and the sensitivities of stomatal conductance and photosynthesis to VPD. The results from the modelling approach used in this study are in good agreement with previously published estimates of the parameters for *Nothofagus*, and are particularly relevant since they were obtained from plants growing in a natural area.

Problems with condensation in the leaf chamber during low light conditions limited the amount of data collected at low light intensities. The lack of these data made it impossible to add a light compensation term into the model and also means that the light saturation points for stomatal conductance should be treated only as a rough estimate since the amount of data at light intensities lower than a PPFD of 400 μmol m^{-2} s^{-1} was limited. The parameter estimates were obtained using non-linear least squares regression techniques to fit the models developed in chapter 3 to photosynthetic and stomatal conductance data, and would have been biased due to the irregular distribution of the data. The approach used by this study was however a major improvement on other analysis methods used previously to analyze porometry data (Discussed in Chapter 3). The distribution of the data varied seasonally as the ambient conditions changed due to weather conditions and this may have have influenced some of the seasonal differences. This problem is intrinsic with any type of ambient porometer and could only be improved in the field by using a climatized cuvette. Such an approach would allow the accurate determination of A_{max} and g_{max} which then could be used as fixed parameters in the model improving its accuracy. If possible this approach should be utilized in future studies.

6. STATION CREEK GAS EXCHANGE MEASUREMENTS.

6.1 INTRODUCTION.

The indigenous forest in the Maruia region is predominantly of mixed *N. fusca* and *N. menziesii*. The Station Creek experimental area was used in this project to obtain a comparison of environmental variables in open and sub-canopy sites (Chapter 4). The management trials which commenced in the early 1970's have left areas of regenerating *Nothofagus* seedlings and saplings of various age. These plants have regenerated from seed in the open areas left after logging and have not been manipulated apart from the oldest stands which have been thinned. The young saplings growing in the open at Station Creek were in a phase of rapid growth similar to those growing in the FRI nursery at Rangiora (Chapter 5). The objectives for making gas exchange measurements of these saplings at Station Creek were essentially the same as those listed for the Rangiora measurements (Chapter 5). The Station Creek saplings however also provided an opportunity to compare the gas exchange of naturally growing plants with those in the managed nursery at Rangiora. In Chapter 5 it was concluded that moderate water stress during the early part of the 1984-5 season reduced the rates of gas exchange in both *N. fusca* and *N. menziesii*. The Maruia region is not usually subjected to drought conditions and the spring and early summer of the 1984-5 season were considerably wetter than the mean (Chapter 4). Comparison of the seasonal variation in the gas exchange parameters derived from Station Creek and Rangiora data should determine if water stress reduced the rates of gas exchange in the Rangiora saplings during the 1984-5 season.

6.2 METHODS.

6.2.1 Gas Exchange.

The gas exchange methods and data analysis used on the open site at Station Creek were identical to those used at Rangiora (Chapter 5). Individual saplings were selected for measurement in a logged area near the canopy gap site described in chapter 4, and were mainly less than ten years old.

6.2.2 Xylem Water Potential.

Pre-dawn xylem water potential measurements of foliage samples of both *N. fusca* and *N. menziesii* were conducted at monthly intervals during 1985 using a pressure bomb (Scholander *et al.* 1965).

6.3 RESULTS.

Estimates of A_{max} (Table 6.1) and g_{max} (Table 6.2) were higher in *N. menziesii* than *N. fusca* and declined as the foliage aged. The light saturation points for both photosynthesis and stomatal conductance did not show any distinct seasonal trends

but were lower for stomatal conductance than for photosynthesis. The sensitivity of stomatal conductance to VPD (Table 6.2) ranged between 1.7 and 3.3%. The curve fitting procedure failed to converge with *N. fusca* data from October 1985 and hence no comparison could be made between the March and October data. The photosynthetic sensitivity of *N. menziesii* foliage to VPD was lower in November 1985 than for the other two estimates (February and April), however the stomatal sensitivity (Table 6.2) in November was not significantly different from the February estimate. The April estimate of 3.3% was higher than the other two. The photosynthetic sensitivity of *N. fusca* foliage (Table 6.1) was essentially non existent (-0.7%) whilst the March estimate of 1.45% was not significantly different from the February and April estimates for *N. menziesii* foliage.

The pre-dawn water potential measurements (Fig. 6.1) were lowest during the period from September to December 1985. The lowest measurements were obtained in November with -0.34 MPa for *N. fusca* and -0.38 MPa for *N. menziesii*.

N. fusca		A_{max} (μmol m^{-2} s^{-1})	Q (x1000)	Sat (μmol m^{-2} s^{-1})	D_A (%)	N	F	R^2	CV (%)	SLW (g m^{-2})
March	1985	9.38±0.46	4.51±0.53	511	1.45±0.19	221	60.7	.36	27.3	70.7±4.2
October	1985	7.82±2.73	2.44±1.00	944	-0.73±0.26	55	5.8	.18	28.9	94.0±2.8

N. menziesii		A_{max} (μmol m^{-2} s^{-1})	Q (x1000)	Sat (μmol m^{-2} s^{-1})	D_A (%)	N	F	R^2	CV (%)	SLW (g m^{-2})
February	1985	12.26±0.65	2.42±0.28	751	1.68±0.18	154	46.7	.38	15.5	109.3±4.1
April	1985	11.79±0.59	2.11±0.19	1091	1.67±0.24	148	183.4	.72	15.0	117.8±2.9
October	1985	8.76±0.27	2.32±0.02	1101	0.86±0.96	213	44.2	.30	12.2	106.0±2.4

Table 6.1 Estimates of photosynthetic parameters for *N. fusca* and *N. menziesii* growing on a open site at Station Creek.

(Details as for Table 5.1)

N. fusca		g_{max} (mmol m^{-2} s^{-1})	Q (x1000)	Sat (μmol m^{-2} s^{-1})	D_A (%)	N	F	R^2	CV (%)
March	1985	127.3±4.4	9.7±1.5	235	2.59±0.12	221	94.7	.47	30.5
October	1985		Not Converging						

N. menziesii		g_{max} (mmol m^{-2} s^{-1})	Q (x1000)	Sat (μmol m^{-2} s^{-1})	D_A (%)	N	F	R^2	CV (%)
February	1985	198.4±6.7	10.2±3.7	225	2.03±0.15	154	48.4	.39	17.6
April	1985	204.6±9.9	2.8±0.3	813	3.25±0.19	148	86.6	.54	20.0
October	1985	159.0±3.3	12.1±1.8	190	1.71±0.64	213	158.7	.60	14.1

Table 6.2 Estimates of stomatal parameters for *N. fusca* and *N. menziesii* growing in the open at Station Creek.

(Details as for Table 5.2)

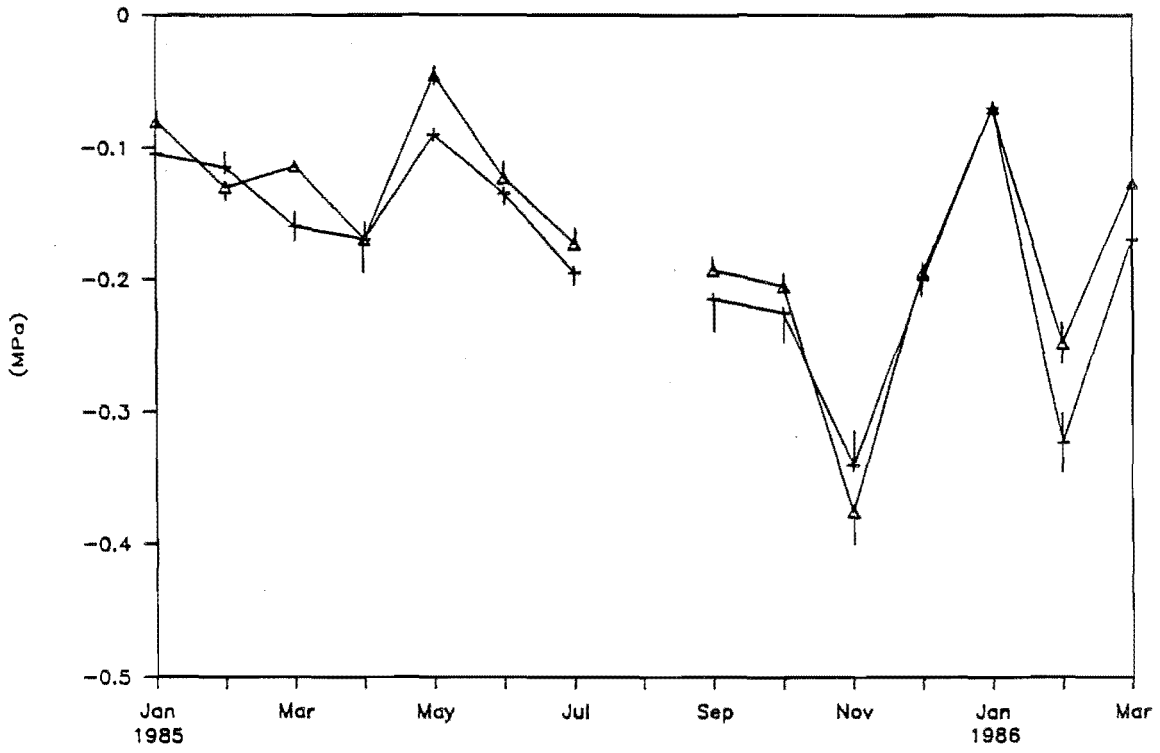

Figure 6.1 Pre-dawn xylem water potential measurements at Station Creek.

Xylem water potential (MPa) was measured using a pressure Bomb (Scholander *et al.* 1965) for *N. menziesii* (△) and *N. fusca* (+). Each point is the mean of at least eight replicates (±1 s.e.).

6.4 DISCUSSION.

The estimates of the gas exchange parameters obtained with Station Creek data were similar to those obtained at Rangiora (Chapter 5), except that the decline in the rates of gas exchange as the foliage aged was lower at Station Creek. A_{max} and g_{max} of young foliage during the 1984-5 season was essentially the same at both sites. By April 1985 the rates of gas exchange of both species at Rangiora were substantially lower than equivalent foliage at Station Creek.

The photosynthetic and Stomatal sensitivity to VPD of both species at Station Creek showed no significant difference between species at the start of the season, but by the end of the season (October, November data) the sensitivity was significantly higher in *N. menziesii*. These trends also occurred at Rangiora and are due to the senescence of *N. fusca* foliage after one season whilst *N. menziesii* will last for up to three.

The main environmental differences between Rangiora and Station Creek was the amount of rainfall. The annual mean rainfall at Springs Junction (15 km south of Station Creek) is three times higher than at Rangiora. The 1984-85 foliage at Rangiora developed during a period of below average rainfall whilst at Station Creek the spring was slightly wetter than usual (Chapter 4). In chapter 5 it was concluded that moderate water stress had reduced the rates of gas exchange of both species growing at Rangiora during the 1984-85 season. The results in this chapter confirm this conclusion. Pre-dawn water potentials during January 1985 at Station Creek were around -0.1 MPa for both species, whilst at Rangiora both species were below -0.6 MPa. The data from both Rangiora and Station Creek show that the rates of gas exchange declined as the foliage aged, but the Rangiora data showed an additional reduction that can only be attributed to environmental differences between the two sites.

7. SUB-CANOPY GAS EXCHANGE.

7.1 INTRODUCTION.

Nothofagus seedlings growing under closed canopy form a suppressed 'advance growth pool' (Wardle 1984). If a break occurs in the canopy the seedlings may respond to the changes in the environment with increased rates of growth. The magnitude of the changes in the sub-canopy environment depends on the size of the canopy gap. Small scale disturbance such as the death or windthrow of a few trees form small canopy gaps with environmental characteristics intermediate to those of the sub-canopy and open environments. Large scale disturbance such as mass movement, a large windthrow or clearfell logging produce an environment similar to that of a large open area. The environmental conditions under a closed *Nothofagus* canopy are characterized by low light flux, daily temperature variation, water vapour pressure deficit and water stress (Chapter 4). By contrast on an area of open ground the conditions are of high light flux, temperature variation, VPD and potential water stress.

Seedlings growing under canopy gaps or in the open experience an environment substantially different from those growing under closed canopy. In response the growth rates of seedlings under canopy gaps and in the open may be several times higher than those growing under a forest canopy (Wardle 1984). It might therefore be expected that physiological differences would exist between seedlings subjected to the different environments.

The physiological and morphological differences between plants growing under different light intensities were reviewed by Boardman (1977) and Bjorkman (1981). Shade tolerant plants tend to have adaptations which maximize carbon gain in the low light conditions prevalent under a canopy. Light is the primary environmental factor limiting carbon gain and growth of plants in the canopy understorey (Pearcy 1983). Shade light differs in both quantity and quality from the light incident at the top of the canopy. The spectral composition of shade light has a lower Red/Far-red ratio, and the quantum flux is greatly reduced. PPFD levels under a closed *Nothofagus* canopy tend to be approximately five percent of those at the top of the canopy (Chapter 4, Turton 1982, McCracken *pers comm*). The photosynthetic responses of plants to shade and full sunlight have been compared using a wide range of plant types (Reviewed by Boardman 1977). Light response curves for shade plants are characterized by lower light compensation and saturation points than for sun plants. Similar differences are observed when comparing sun and shade leaves within a species or on the same plant (e.g. Schulze 1970). The stomatal responses to light intensity show similar differences between sun and shade foliage. The spectral differences between sun and shade light have often been ignored in controlled environment studies of sun and shade foliage

(Kwesiga and Grace 1986). There has been little work investigating the physiology of shade plants *in situ* under a natural canopy (Bjorkman and Ludlow 1972, Bjorkman *et al.* 1972, Fetcher *et al.* 1983, Huber 1978, Kuppers 1984, Lebron 1979, Wallace and Dunn 1980).

The comparison of the sub-canopy and open environments (Chapter 4), showed that as well as differences in the light environment, marked differences existed in the temperature and water characteristics of the sites. Under closed canopy and a small canopy gap the daily temperature variation was much lower than on an adjacent open area. The mean daily maximum atmospheric VPD measured beneath the canopy gap was consequently much lower than in the open and would be expected to be even lower under a fully closed canopy. These observations indicate that the potential evaporative losses from plants growing in the open are much higher than for those growing under the canopy. Sun plants and foliage tend to have better developed morphological and physiological adaptations to prevent water loss (Bjorkman 1981) since water tends to be an important factor limiting plant growth in the open.

The stomatal sensitivity to atmospheric VPD is a measure of the amount that stomata close in response to increasing evaporative demand, and is often higher in sun than in shade foliage. The stomatal sensitivity of shade foliage of *Fagus sylvatica* was found by Schulze (1970) to be lower than that of sun foliage on the same tree. Similar results have been reported by Benecke and Evans (1986) for *Nothofagus truncata*. There has been no comparison of the stomatal sensitivity to VPD for beech seedlings or saplings growing either in the open or under closed canopy as previous studies have been confined to foliage growing on adult trees. If there is any difference in the stomatal sensitivity of shade and sun grown *Nothofagus* seedlings it would be expected that shade foliage would have lower sensitivity. If shade grown seedlings are not well adapted to prevent water loss it is possible that when canopy opening occurs they will experience extreme water stress due to the higher evaporative demand. This may explain why seedling mortality is high in large open areas, away from the shelter of the canopy. It can be hypothesized that the low stomatal sensitivity to VPD of shade grown seedlings will limit *Nothofagus* regeneration to environments which are modified by the presence of a partial canopy such as canopy gaps or on open areas near the edge of the canopy. Estimates of stomatal and photosynthetic sensitivity to VPD have been obtained for *N. fusca* and *N. menziesii* saplings growing at Rangiora and Station Creek (Chapters 5 and 6). The objectives of gas exchange measurements under the canopy at Station Creek were to obtain similar estimates for suppressed sub-canopy seedlings of *N. fusca* and *N. menziesii* and to compare them with seedlings growing under a canopy gap and with the estimates obtained in chapters 5 and 6.

7.2 METHODS.

7.2.1 Gas Exchange.

The light intensity beneath the canopy was less than 50 μmol m^{-2} s^{-1} for most of the daylight hours during the experimental period. In order to obtain higher light intensities for gas exchange measurements four portable lighting units were constructed. The lamps used were 400w Thorn Kolararc metal halide lamps mounted horizontally beneath an aluminum reflector and above a static water screen consisting of between one and two cm depth of water and 4mm of clear perspex. The lamps produced a spectrum similar to that of normal sunlight with the water screen reducing the thermal load and ultra-violet output from the lamps. Gas exchange measurements were made using the LI-COR LI-6000 portable photosynthesis system as described in chapter 2. All measurements were made at light intensities above 850 μmol m^{-2} s^{-1} which is well above the light saturation point for *Nothofagus* foliage (Benecke and Evans 1986, Reed and Hill 1985). PPFD levels were measured at foliage level within the chamber using a LI-COR LI-190 quantum sensor before each set of gas exchange measurements. The lamp was placed above the foliage for at least 30 minutes before the first gas exchange measurements were obtained. The flow rate through the water by-pass and CO_2 analyzer was between 5 and 10 cm^3 s^{-1} in an attempt to maintain the relative humidity constant in the chamber. The low wind conditions prevalent under the canopy created a problem when making gas exchange measurements with the porometer. On several days there was very little air movement and high CO_2 concentrations occurred where people were working. On these days the effect was minimized by staying well clear of the leaf chamber and when necessary pumping CO_2 free air into the chamber to reduce the CO_2 concentration to between 340 and 350 μmol mol^{-1}.

The LI-6000 was programmed to record ten point measurements at preset intervals of between 10 and 20 seconds and store them as a 'page' of data. A series of ten 'pages' were collected for each twig before changing to the next sample. The twig was cut from the seedling after the final series of measurements and placed in cold storage until measurements of leaf area could be obtained. The projected leaf area was measured using a Delta-T leaf area meter (Delta-T devices, 128 Low Road, Burwell, Cambridge.). All gas exchange measurements are expressed on the basis of projected (one sided) area. The foliage was then dried at 70°C and weighed. The specific leaf weight was calculated as the foliage weight divided by the total projected foliage area. The dried foliage was ground into a powder for subsequent nitrogen analysis using an modified micro Kjeldahl method (Nicholson 1984).

7.2.2 Regression analysis.

The experimental procedures used with the sub-canopy seedlings resulted in the gas exchange data being collected from only light saturated foliage. The main environmental factor affecting the stomatal conductance and photosynthesis was therefore the leaf-air vapour pressure deficit and the regression models used in chapters 5 and 6 were modified to remove the light response.

$$A = A_{max} (1 - D_A(V - 5)) \qquad \text{(eqn. 7.1)}$$

$$g_s = g_{max} (1 - D_g(V - 5)) \qquad \text{(eqn. 7.2)}$$

The models used for the sub-canopy data (eqn 7.1 and 7.2) assume that the stomatal conductance and photosynthetic rate were light saturated and that the variation in the data was attributable to the stomatal response to VPD. The sensitivity of stomatal conductance D_g and photosynthesis D_A to VPD is assumed to be linear over the VPD range normally observed (0 to 30 mPa $Pa^{-1)}$ and to be saturated at a VPD of 5 mPa Pa^{-1} (Benecke and Evans 1986). The data were filtered to remove any data with VPD above 30 mPa Pa^{-1} before the model was fitted using linear least squares regression. The residuals from the regression equation were scanned for extreme values which were checked against the original data. If the reason for the high residual could be determined, it was either removed from the data or the error corrected. The usual reason for data being removed was that the foliage had been damaged by a previous measurement either physically or by high temperature. The regression model was then applied to the corrected data. A separate regression equation was computed for each species and foliage type and the slope (the sensitivity to VPD) of the equations were tested for equality using analysis of variance (Sokal and Rohlf 1981). When there was significant differences ($P < 0.05$) between the regression coefficients, minimum significant differences were computed using the T' method (Sokal and Rohlf 1981).

7.3 RESULTS.

7.3.1 Photosynthesis.

The results from the gas exchange measurements are summarized in tables 7.1 and 7.2. Estimates of the maximum rates of photosynthesis (A_{max}) in the current season's foliage of *N. menziesii* were higher than that for *N. fusca* under both closed canopy and the canopy gap (Table 7.1). The foliage of both species growing beneath the canopy gap had higher maximum rates of photosynthesis than those growing under the fully closed canopy. Comparison of the A_{max} estimates between different season's foliage for *N. menziesii* show no clear pattern. Current season's foliage growing under closed canopy in February had higher A_{max} estimates than the estimate for old season's foliage, however the estimate obtained during March was the lowest obtained under closed canopy. In contrast, the A_{max} of old foliage growing under the canopy was the highest estimate obtained from any foliage type. The coefficients of determination (R^2) tended to be lower for *N. fusca* than for *N. menziesii* which had R^2 values exceeding 0.70 in all but one month's data. The amount of variation explained by the regression equations for *N. fusca* during March was particularly low.

The sensitivity of photosynthesis to VPD (D_A) was similar in both species For *N. fusca* the sensitivity was higher under closed canopy, however for *N. menziesii* there was no significant difference between the two sites.

The specific leaf weight of the foliage used for the gas exchange measurements was higher in *N. menziesii* than in *N. fusca* (Table 7.1). The foliage of both species tended to have higher specific leaf weights when growing under the canopy gap, particularly early in the growing season. Foliar nitrogen concentrations (Table 7.1) were higher in *N. menziesii* than *N. fusca* and in seedlings growing under the canopy gap than under closed canopy.

7.3.2 Stomatal Conductance.

The maximum stomatal conductance (g_{max}) was higher in *N. menziesii* foliage than in *N. fusca* (Table 7.2). In both species g_{max} was considerably higher in plants growing under the canopy gap than under closed canopy. G_{max} of old *N. menziesii* foliage growing under closed canopy was lower than new foliage but the difference was reversed under the canopy gap. The R^2 values for the *N. fusca* regression equations were higher than for the equivalent photosynthesis data, whilst the R^2 values for *N. menziesii* were lower.

The stomatal sensitivity to VPD (Table 7.2) was higher than the photosynthetic sensitivity (Table 7.1). There were no marked differences between species or between canopy gap and closed canopy foliage.

N. fusca	A_{max} (μmol m^{-2} s^{-1})	D_A (%)	N	R^2	CV (%)	SLW (g m^{-2})	SNC (mmol m^{-2})
Closed Canopy							
February	4.83±0.26	$3.27\pm0.40_b$	61	.53	20.76	42.7±1.1	46.1±1.4
March	5.21±0.32	$3.24\pm0.53_b$	80	.32	21.28	40.9±2.3	
Canopy Gap							
January	8.34±0.35	$2.34\pm0.26_{ab}$	66	.57	11.47	50.3±1.0	63.9±2.9
March	5.99±0.16	$1.09\pm0.26_a$	80	.19	8.48	45.3±4.4	

N. menziesii	A_{max} (μmol m^{-2} s^{-1})	D_A (%)	N	R^2	CV (%)	SLW (g m^{-2})	SNC (mmol m^{-2})
Closed Canopy							
(Old Foliage)							
December	6.56±0.13	$2.25\pm0.20_{ab}$	30	.82	5.99	92.1±3.5	57.1±1.5
February	6.76±0.19	$2.81\pm0.18_b$	80	.75	14.97	85.2±2.2	
(New Foliage)							
February	7.22±0.18	$2.70\pm0.15_b$	70	.82	11.27	73.7±0.5	65.6±3.2
March	6.44±0.16	$3.22\pm0.22_b$	54	.80	10.02	69.8±2.5	
Canopy Gap							
(Old Foliage)							
January	10.19±0.55	$3.67\pm0.45_b$	50	.58	16.89	84.5±1.2	76.5±3.0
(New Foliage)							
January	9.20±0.23	$2.53\pm0.16_b$	30	.90	8.77	84.2±2.7	74.9±3.8
March	9.41±0.17	$2.57\pm0.18_b$	80	.72	6.30	71.0±5.1	

Table 7.1 Photosynthetic characteristics of *N. fusca* and *N. menziesii* seedlings growing under closed canopy and a canopy gap at Station Creek between December 1985 and March 1986.

The estimates of maximum photosynthetic rate (A_{max}) and photosynthetic sensitivity to VPD (D_A) were obtained by applying eqn. 7.1 to gas exchange data obtained using the LI-COR LI-6000 portable photosynthesis system. Mean sensitivities (D_A) that are followed by the same letter are not significantly different ($P<0.05$) as determined by a multiple range test. The foliage was illuminated to provide light intensities above saturation point. The number of data points (N), and coefficients of determination (R^2) and variation (CV) indicate the goodness of fit for the combinations of foliage type and time of year. The specific leaf weight (SLW) and nitrogen content (SNC) were determined after the foliage was dried at 70°C. The nitrogen data were pooled within each foliage type.

N. fusca	g_{max} (mmol m^{-2} s^{-1})	D_A (%)	N	R^2 (%)	CV
Closed Canopy					
February	107.6±4.5	$3.27\pm0.31_{ab}$	61	.65	16.24
March	96.6±2.5	$2.94\pm0.22_{ab}$	80	.69	8.36
Canopy Gap					
January	144.9±7.8	$2.58\pm0.33_{a}$	66	.49	15
March	138.9±4.2	$2.60\pm0.28_{a}$	80	.51	11.38

N. menziesii	g_{max} (mmol m^{-2} s^{-1})	D_A (%)	N	R^2 (%)	CV
Closed Canopy					
(Old Foliage)					
December	155.0±3.6	$3.62\pm0.23_{ab}$	30	.90	8.19
February	163.4±4.2	$3.52\pm0.17_{ab}$	80	.85	16.13
(New Foliage)					
February	184.4±7.0	$3.35\pm0.23_{ab}$	70	.75	20.93
March	175.4±3.2	$4.15\pm0.17_{b}$	54	.92	8.62
Canopy Gap					
(Old Foliage)					
January	257.2±0.6	$4.30\pm0.31_{b}$	50	.80	13.33
(New Foliage)					
January	193.5±0.1	$3.02\pm0.17_{ab}$	30	.92	10.31
March	215.4±0.8	$2.92\pm0.27_{ab}$	80	.60	9.90

Table 7.2 Maximum stomatal conductance and stomatal sensitivity to VPD of *N. fusca* and *N. menziesii* seedlings growing under closed canopy and a canopy gap at Station Creek between December 1985 and March 1986.

The estimates of maximum stomatal conductance (g_{max}) and stomatal sensitivity to VPD (D_g) were obtained by applying eqn. 7.2 to gas exchange data obtained using the LI-COR LI-6000 portable photosynthesis system. (Other details as for Table 7.1)

7.4 DISCUSSION.

The techniques used to describe the gas exchange of seedlings growing in the sub-canopy environment were very successful, particularly considering the limitations of the equipment and the adverse environmental conditions. The main problems apparent during the study were related to the nature of the sub-canopy environment. Gas exchange measurements were limited to periods in which the sub-canopy foliage was dry. The LI-6000 was capable of measuring the photosynthesis of wet foliage but the Vaisala humidity sensor would have been affected and takes well over a day to recover after exposure to high humidities. If this had been allowed to occur it would have altered stomatal conductance measurements taken on the next dry day, and would have reduced the repeatability of measurements. The inability to control leaf temperature means that the parameter estimates obtained from the regression models will be biased due to temperature effects. It is however unlikely that the effect was large since *Nothofagus* species tend to have a broad temperature optimum for photosynthesis and stomatal conductance. (Benecke and Havranek 1980a).

The A_{max} estimates from canopy gap *N. fusca* foliage agree with the estimates obtained with saplings at Rangiora and Station Creek in chapters 5 and 6 as well as with data from *N. truncata* (Benecke and Evans 1986). The estimates for *N. menziesii* are in agreement with those obtained in chapters 5 and 6 and are similar to those reported by Benecke and Havranek (1980a) for *N. solandri* var. *cliffortioides*. The nitrogen content of the foliage was related to the specific leaf weight and was higher in the foliage of *N. menziesii*. The differences between A_{max} in *N. menziesii* and *N. fusca* can be explained by the nitrogen and leaf weight data. Benecke and Evans (1986) used specific leaf weight as a parameter in their photosynthetic model for a stand of *N. truncata*. The relationship between foliar nitrogen content and photosynthetic rate is well documented (Chapin *et al.* 1987).

The gas exchange system used in this study was not ideal because of the problems encountered whilst working in the sub-canopy environment. It would have been preferable to have used a climatized cuvette which would have permitted the determination of factor response curves and produced non-biased estimates from the regression model. Such a system would also be able to operate during moist periods if the humidity sensor was replaced by dew point mirrors or by a heated viasala sensor, and if suitable operational precautions were taken.

Any attempt to measure to gas exchange of plants growing under a forest canopy is made difficult by the nature of the sub-canopy environment. The climate of the West Coast of the South Island of New Zealand is an additional problem due to the wet conditions which can prevail at certain times of the year. The design of any field experiment is constrained by these factors and is a compromise between

what is desirable, and that which is technically possible within the limits of the equipment.

8. DISCUSSION.

8.1 GENERAL.

Nothofagus forests compromise 68% of New Zealand's remaining indigenous forests. They are extremely important for environmental, economic and social reasons. It is therefore surprising that very little research has been conducted on the ecology of these *Nothofagus* forests. The maintenance of the forest canopy is dependent on the process of regeneration to replace canopy trees after their death. Most canopy gaps in *Nothofagus* forest are filled by the rapid growth of seedlings which were present on the forest floor before the gap occurred (Wardle 1984). This study identified two areas where research was required to improve the understanding of *Nothofagus* regeneration. The first was to compare environmental parameters under closed canopy, a canopy gap, and an open area. The second was to measure the physiological responses of suppressed seedlings to a canopy gap and to compare these with plants growing in the open.

8.2 THE ENVIRONMENT.

There have been no previous attempts to compare a range of environmental parameters between closed canopy, canopy gap and open environments for New Zealand's *Nothofagus* forests. The measurements conducted at Station Creek (Chapter 4) identified the main differences between these environments and their probable effects on seedling growth (Table 8.1). The canopy gap environment falls between the two extremes of sub-canopy and open site and will depend on the size of the gap, height of the canopy, and time of year.

	OPEN SITE	SUB-CANOPY
Light flux	High Non-limiting	10% of open site Limiting
Temperature variation	High Potentially limiting	Low Non-limiting
Humidity	Low Limiting	High Non-limiting
Water availability	Soil drying in summer Potentially limiting	High Non-limiting

Table 8.1 Environmental parameters limiting seedling growth on the sub-canopy and open environments.

The canopy gap environment is the most favourable for regeneration. Light intensities under a small canopy gap at Station Creek were 25% of full sunlight during summer. This value is close to the optimum light intensity for *Nothofagus* regeneration reported by Wardle (1970) and June and Ogden (1975). Turton (1982) in a series of measurements across a canopy gap in *N. solandri* forest obtained relative light intensities of 20% which were correlated with vigorous regeneration. His measurements were made during early winter and the relative intensities would have been higher during summer. Water availability in the upper layers of soil was limited during summer on the open site at Station Creek, however under the canopy gap the soil was moist for the entire season. Plants growing on the open site were subjected to extremely high temperatures in summer and cold temperatures in winter which may explain the high proportion of shoot tip death observed in the open.

Seedling establishment and growth on open sites are limited by extremes of temperature and soil drying during summer. Under fully closed canopy, seedling growth is limited by low light intensity.

8.3 GAS EXCHANGE.

The environmental measurements suggest that under closed canopy light is limiting for seedling growth, and that in the open, water availability is likely to be more important. The objectives of porometry measurements in this study were to compare the rates of gas exchange under contrasting environments, and to identify any ecological adaptations to the closed canopy or open sites. The measurements concentrated on two aspects, firstly the maximum rates of photosynthesis and stomatal conductance, and secondly the stomatal and photosynthetic sensitivity to VPD. The stomatal sensitivity to VPD is a measure of the stomatal control of transpirational water loss. Plants which are well adapted to dry environments tend to have higher stomatal sensitivity than do plants from moist habitats (Schulze and Hall 1982).

The hypothesis proposed at the start of the study suggested that stomatal sensitivity to VPD should be higher in the open as was found by Benecke and Evans (1986) with adult *N. truncata* foliage. No significant differences were detected between seedlings growing under closed canopy or canopy gap (Chapter 7) and these data were in broad agreement with the estimates from saplings growing in the open at both Rangiora and Station Creek (Chapters 5 and 6). The plants in this study did however show other physiological adaptations to the environment, since A_{max} and g_{max} were higher in the open than under closed canopy.

The difficulties in measuring stomatal sensitivity to VPD with the porometer used in this study have been discussed in chapters 5 to 7. The irregular distribution of data may have influenced the sensitivity estimates but it is unlikely that such a systematic error would have masked any major differences between species or foliage types. It must therefore be concluded that differences in the stomatal sensitivity to VPD were not as great as expected or else did not exist. The photosynthetic sensitivity to VPD is mediated by the stomatal response and also showed no significant differences between species or foliage types.

The explanation of these results may lie in the general ecology of *Nothofagus* seedlings and saplings. *Nothofagus* regenerates on sites ranging from under closed canopy to recently exposed bare mineral soils. The majority of adult trees in a forest are derived from the suppressed seedling pool, although regeneration under more extreme environments does occasionally occur. The stomatal sensitivity to VPD did not vary over a wide range of contrasting environments or between *N. menziesii* and *N. fusca*. This indicates that the response is a generalized adaptation for the wide range of environments in which *Nothofagus* seedlings may establish. This conclusion implies that for *Nothofagus* seedlings to survive under extreme environments, they require additional adaptations to prevent water loss. During periods of moderate water stress at both Rangiora and Station Creek, the trees shed a proportion of their current season's foliage. This would have lowered

the rate of water loss by reducing the total foliage area. This phenomenon was also observed with *N. truncata* during a drought in north west Nelson (Benecke *pers comm*.). The effect on growth of a reduction in foliage area is dependent on the age of the tree. In adult trees the foliage represents a small proportion of the total biomass, while in seedlings the loss of carbon and nutrients represents a large proportion of the total reserves, and therefore they will be more susceptible to drought. The gas exchange data from Rangiora demonstrated that water stress can reduce the rates of photosynthesis in both *N. fusca* and *N. menziesii*. The growth of a *Nothofagus* seedlings in the open is limited by water availability and they are unable to compete with faster growing ruderal species. These conclusions explain the patterns of regeneration observed with *Nothofagus*. The optimal conditions for seedling growth occur under canopy gaps with environmental conditions intermediate to the extremes observed under fully closed canopy and in the open. The generalized adaptations of *Nothofagus* seedlings allow establishment on extreme sites, but carbon uptake is limited by light under closed canopy, and by water in the open. Seedlings which become established under extreme environments can only survive in the absence of more rapidly growing competing species.

Baylis (1980) suggested that mycorrhizae play an important role in *Nothofagus* regeneration. His experiments need to be repeated since the experimental design was inappropriate and did not rule out alternative conclusions. In addition to improving nutrient uptake the mycorrhizal association would also increase the amount of water available to the plant by exploiting a larger root zone.

The nitrogen estimates were in good agreement with those of Adams (1976) and Heine (1973). The nitrogen content per unit leaf area was higher in *N. menziesii*, but if these data are converted to a weight percentage *N. fusca* was higher than *N. menziesii*.

The estimates of A_{max} and g_{max} were in good agreement with other studies (Benecke and Evans 1986, Benecke and Havranek 1980a, Benecke and Nordmeyer 1982, Read and Hill 1985). The observation that A_{max} of *N. menziesii* was consistently higher than *N. fusca* was contrary to the prediction at the start of the study. This has been explained by the higher specific leaf weight and nitrogen content of *N. menziesii* foliage. The correlation between nitrogen content and A_{max} is well documented and was recently reviewed (Chapin *et al.* 1987). The importance of specific leaf weight in determining the photosynthetic rate of *Nothofagus* foliage was recognized by Benecke and Evans (1986) who included specific leaf weight in their photosynthetic model for a stand of *N. truncata*. The photosynthetic rate of *N. menziesii* is similar to that of *N. solandri* var. *cliffortioides* (Benecke and Havranek 1980a) which has a similar specific leaf weight (Benecke and Havranek 1980b).

8.4 FUTURE RESEARCH.

This project is the first to investigate physiological aspects of the ecology of *N. fusca* and *N. menziesii*. It has been possible to demonstrate physiological differences between the species, which indicates that the system is suitable for further, more intensive research. Some of the results were contrary to those predicted at the start of the study and further work is required to clarify the differences between species. Differences in photosynthetic rate do not account for the higher growth rate of *N. fusca* since *N. menziesii* had consistently higher maximum rates of photosynthesis. The carbon and nitrogen partitioning of *Nothofagus* seedlings and saplings requires investigation and a comparison between *N. menziesii* and *N. fusca* would be likely to produce useful information. There are several aspects which would need to be emphasized in any such study.

1. A comparison of the energy requirements (Costs) between the short lived foliage of *N. fusca* and *N. menziesii* which maintains it's foliage for up to three years.
2. A comparison of nitrogen allocation between species.
3. A detailed study of the root system.
4. An investigation of the effects of water and temperature stress on photosynthesis and partitioning.

Gas exchange studies should be used in conjunction with these studies to investigate the effects of water and temperature stress on the growth of saplings, as this is particularly relevant to forest management. Further gas exchange work, should if possible be conducted using climatized cuvettes to improve the data collected for modelling purposes.

8.5 IMPLICATIONS FOR *NOTHOFAGUS* MANAGEMENT.

The management of *Nothofagus* forests for sustained yield production has occasionally resulted in poor regeneration after logging. One of the main reasons for the failure has been that faster growing 'weed' species have overtopped the *Nothofagus* seedlings. Another has been the death of saplings growing in the open.

The ecological conclusions from this study can be used to suggest modifications to the current management practices which could improve the amount of regeneration occurring after logging. The finding that there was no significant difference in the stomatal sensitivity to VPD between seedlings growing in the shade and open has two important implications for management.

The first is that whilst seedlings are able to establish under a wide range of environmental conditions, care must be taken to prevent extremes. In practice this means leaving as much overstorey as is possible to create an environment

conducive to regeneration. The overstorey has two main effects, firstly to reduce extremes of temperature and evaporative demand, and secondly to reduce the light intensity thereby inhibiting the growth of competing 'weed' species. The amount of overstorey left, will in practice also be determined by economic constraints as well as considerations of forest health.

The second implication for management is that seedlings growing in the open will need well developed root systems. The development of an adequate root system after logging is often inhibited by the disruption of soil structure by heavy machinery. In several of the trial areas at Station Creek there was virtually no regeneration where the soil had been compacted during logging. The only remedy for this problem is to make every effort during logging to prevent soil damage, as attempts to plant nursery seedlings on these areas have tended to fail. If supplementary planting is considered necessary after logging, the seedlings will need additional shading and good root development to increase survival.

The second finding of importance is that there are distinct physiological differences between *N. fusca* and *N. menziesii*. The maximum stomatal conductance and photosynthetic rates were significantly higher in *N. menziesii* than *N. fusca*. This implies that there are differences in carbon partitioning and growth costs since *N. fusca* is the faster growing species. The management regime could manipulate these differences to select for a higher proportion of one species in the sapling population following logging. Several lines of research have been suggested and results from such work may develop new management strategies to be used for species selection.

REFERENCES.

Adams, J.A., 1976. Nutrient requirements of four *Nothofagus* species in north Westland, New Zealand, as shown by foliar analysis. *New Zealand Journal of Botany*, **14**:211-23.

Bates, L.M., Hall, A.E., 1982. Diurnal and seasonal responses of stomatal conductance for Cowpea plants subjected to different levels of environmental drought. *Oecologia (Berlin)*, **54**:304-08.

Baylis, G.T.S., 1980. Mycorrhizas and the spread of beech. *New Zealand Journal of Ecology*, **3**:151-53.

Beadle, C.L., Turner, N.C., Jarvis, P.G., 1978. Critical water potential for stomatal closure in Sitka Spruce. *Physiologia Plantarum*, **43**:160-65.

Benecke, U., 1985. Tree respiration in steepland stands of *Nothofagus truncata* and *Pinus radiata*, Nelson New Zealand. *in:* Turner, H., Tranquillini, W., (eds.), Establishment and tending of subalpine forest: Research and Management. p61-70.

Benecke, U., Evans, G., 1986. Growth and water use in hard beech (*Nothofagus truncata*) in temperate hill country, Nelson, New Zealand. Proceedings: International Symposium on Temperate Forest Ecosystem Management and Environment Protection. Changbai Mountain Research Station of Forest Ecosystems, Academia Sinica, China. (in press).

Benecke, U., Havranek, W.M., 1980a. Gas-exchange of trees at altitudes up to timberline, Craigieburn range, New Zealand. *in:* Benecke, U., Davis, M.R., (eds.), Mountain Environments and Subalpine Tree Growth. Forest Research Institute, New Zealand Forest Service, Technical Paper No. 70. p195-212.

Benecke, U., Havranek, W.M., 1980b. Phenological growth characteristics of trees with increasing altitude, Craigieburn Range, New Zealand. *in:* Benecke, U., Davis, M.R., (eds.), Mountain Environments and Subalpine Tree Growth. Forest Research Institute, New Zealand Forest Service, Technical Paper No. 70. p155-174.

Benecke, U., Havranek, W.M., McCracken, I.J., 1976. Comparative study of water use by tree species in a mountain environment. Proceedings Soil and Plant Water Symposium, Palmerston North, New Zealand. p191-199.

Benecke, U., Nordmeyer, A.H., 1982. Carbon uptake and allocation by *Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole and *Pinus contorta* Douglas ex Loudon ssp. *contorta* at montane and subalpine altitudes. *in:* Waring, R.H. (ed.), Carbon uptake and allocation in subalpine ecosystems as a key to management. Proceedings of an IUFRO workshop P.1.07-00 Ecology of Subalpine Zones. p9-21.

Bjorkman, O., 1981. Responses to different quantum flux densities. *in:* Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (eds.), Encyclopedia of Plant Physiology Volume 12A. Physiological Plant Ecology I. Responses to the physical environment. Springer-Verlag, Berlin. p57-107.

Bjorkman, O., Ludlow, M.M., 1972. Characterization of the light climate on the floor of a Queensland rainforest. *Carnegie Institute of Washington, Yearbook*, **71**:85-94.

Bjorkman, O., Ludlow, M.M., Morrow, P.A., 1972. Photosynthetic performance of two rainforest species in their native habitats and analysis of their gas exchange. *Carnegie Institute of Washington, Yearbook*, **71**:94-102.

Boardman, N.K., 1977. Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology*, **28**:355-77.

Chapin, F.S. III., Bloom, A.J., Field, C.B. Waring, R.H., 1987. Plant responses to multiple environmental factors. Physiological ecology provides tools for studying how interacting environmental resources control plant growth. *Bioscience*, **37**:49-57.

Cockayne, L., 1926. Monograph on the New Zealand beech forests. Part 1. The ecology of the forests and the taxonomy of the beeches. *New Zealand Forest Service Bulletin*, **4**. 71p.

Cockayne, L., 1928. Monograph on the New Zealand beech forests. Part 2. The forests from the practical and economic standpoints. *New Zealand Forest Service Bulletin*, **4**. 59p.

Conway, G.R., Glass, N.R., Wilcox, J.C., 1970. Fitting nonlinear models to biological data by Marquardt's algorithm. *Ecology*, **51**:504-07.

Cowan, I.R., 1977. Stomatal behaviour and environment. *Advances in Botanical Research*, **4**:117-228.

Davies, W.J., Kozlowski, T.T., 1974. Stomatal responses of five woody angiosperms to light intensity and humidity. *Canadian Journal of Botany*, **52**:1525-34.

De Jong, T.M., Doyle, J.F., 1985. Seasonal relationships between leaf nitrogen content (photosynthetic capacity) and leaf canopy light exposure in peach (*Prunus persica*). *Plant, Cell and Environment*, **8**:701-706.

Ehleringer, J.R., Cook, C.S., 1984. Photosynthesis in *Encelia farinosa* Gray in response to decreasing leaf water potential. *Plant Physiology*, **75**:688-93.

Farquhar, G.D., 1978. Feedforward responses of stomata to humidity. *Australian Journal of Plant Physiology*, **5**:787-800.

Farquhar, G.D., Schulze, E.-D., Kuppers, M., 1980. Response to humidity by stomata of *Nicotiana glauca* L. and *Corylus avellana* L. are consistent with the optimization of carbon dioxide uptake with respect to water loss. *Australian Journal of Plant Physiology*, **7**:315-27.

Farquhar, G.D., Sharkey, T.D., 1982. Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology*, **33**:317-45.

Farquhar, G.D., von Caemmerer, S., 1982. Modelling of photosynthetic responses to environmental conditions. *in:* Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (eds.), Encyclopedia of Plant Physiology Volume 12B. Physiological Plant Ecology II. Water relations and Carbon Assimilation. Springer-Verlag, Berlin. p549-87.

Farquhar, G.D., Wong, S.C., 1984. An empirical model of stomatal conductance. *Australian Journal of Plant Physiology*, **11**:191-210.

Fetcher, N., Strain, B.R., Oberbauer, S.F., 1983. Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. *Oecologia (Berlin)*, **58**:314-19.

Franklin, D.A., 1974. Beech (*Nothofagus*) silviculture in the South Island. *Proceedings of the New Zealand Ecological Society*, **21**:17-20.

Franklin, D.A., Beveridge, A.E., 1975. Forest management and research in indigenous production forests. *New Zealand Journal of Forestry*, **20**:63-71.

Gleason, C.D., 1982. Prospects for intensive management of West Coast beech Forest. *New Zealand Journal of Forestry*, **27**:77-88.

Gollan, T., Turner, N.C., Schulze, E.-D., 1985. The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content. III. In the sclerophyllous woody species *Nerium oleander*. *Oecologia (Berlin)*, **65**:356-62.

Gutschick, V.P,. Barron, M.H,. Waechter, D.A,. Wolf, M.A., 1985. Portable monitor for solar radiation that accumulates irradiance histograms for 32 leaf mounted sensors. *Agricultural and Forest Meteorology*, **33**:281-90.

Heine, M., 1973. A comparison of nutrients in leaves and litter of red, silver and mountain beech. *Mauri Ora*, **1**:55-60.

Hellkvist, J., Hillerdal-Hagstromer, K., Mattson-Djos, E., 1980. Field studies of water relations and photosynthesis in Scots pine using manual techniques. *in:* Persson, T., (ed.), Structure and function of northern coniferous forests - An ecosystem study. *Ecological Bulletin (Stockholm)*, **32**:183-204.

Huber, O., 1978. Light compensation point of vascular plants of a tropical cloud forest and an ecological interpretation. *Photosynthetica*, **12**:382-390.

Hutmacher, R.B., Krieg, D.R., 1983. Photosynthetic rate control in cotton. Stomatal and nonstomatal factors. *Plant Physiology*, **73**:658-661.

Jane, G.T., Green, T.G.A., 1983. Utilisation of pressure-volume techniques and non-linear least squares analysis to investigate site induced stresses in evergreen trees. *Oecologia (Berlin)*, **57**:380-90.

Jarman, P.D., 1974. The diffusion of carbon dioxide and water vapour through stomata. *Journal of Experimental Botany*, **25**:927-36.

Jarvis, P.G., 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philosophical Transactions of the Royal Society of London. Series B.*, **273**:593-610.

Jarvis, P.G., Catsky, J., Eckardt, F.E., Koch, W., Koller, D., 1971. General principles of gaseometric methods and the main aspects of installation design. *in:* Sestak, Z., Catsky, J., Jarvis, P.G., Plant photosynthetic production. Manual of methods. Dr W. Junk N.V., The Hague. p49-110.

Jarvis, P.G., Morison, J.I.L., 1981. The control of transpiration and photosynthesis by the stomata. *in:* Jarvis P.G., Mansfield, T.A., Stomatal Physiology, Cambridge University press, Cambridge. p248-79.

Jones, H.G., 1985. Partitioning stomatal and non-stomatal limitations to photosynthesis. *Plant, Cell and Environment*, **8**:95-104.

June, S.R., Ogden, J., 1975. Studies on the vegetation of Mount Colenso, New Zealand. 3. The population dynamics of red beech seedlings. *Proceedings of the New Zealand Ecological Society*, **22**:61-6.

Kaufmann, M.R., 1982a. Leaf conductance as a function of photosynthetic photon flux density and absolute humidity difference from leaf to air. *Plant Physiology*, **69**:1018-22.

Kaufmann, M.R., 1982b. Evaluation of season, temperature, and water stress effects on stomata using a leaf conductance model. *Plant Physiology*, **69**:1023-26.

Kirkland, A., 1961. Preliminary notes on seeding and seedlings in red and hard beech forests of north Westland and the silvicultural implications. *New Zealand Journal of Forestry*, **8**:482-97.

Kirkland, A., 1974. New Zealand Forest Service proposals for management and utilisation of South Island beech forests. *Proceedings of the New Zealand Ecological Society*, **21**:1-4.

Kuppers, M., 1984. Carbon relations and competition between woody species in a Central European hedgerow. I. Photosynthetic characteristics. *Oecologia (Berlin)*, **64**:332-43.

Kuppers, M., Schulze, E.-D., 1985. An empirical model of net photosynthesis and leaf conductance for the simulation of diurnal courses of CO_2 and H_2O exchange. *Australian Journal of Plant Physiology*, **12**:513-26.

Kwesiga, F., Grace, J., 1986. The role of the Red/Far-Red ratio in the response of tropical tree seedlings to shade. *Annals of Botany*, **57**:283-90.

Landsberg, J.J., Ludlow, M.M., 1970. A technique for determining resistance to mass transfer through the boundary layers of plants with complex structure. *Journal of Applied Ecology*, **7**:187-92.

Lange, O.L., Losch, R., Schulze, E.-D., Kappen, L, 1971. Responses of stomata to changes in humidity. *Planta (Berlin)*, **100**:76-86.

Lange, O.L., Meyer, A., 1979. Midday Stomatal Closure observed in apricot (*Prunus armeniaca*) and grapevine (*Vitis vinifera*) under field conditions in spite of non limiting soil-water supply. *Flora (Berlin)*, **168**:511-528.

Lebron, M. L., 1979. An autecological study of *Palicourea riparia* Bentham as related to rain forest disturbance in Puerto Rico. *Oecologia (Berlin)*, **42**:31-46.

LI-COR, 1985. LI-6000 Portable Photosynthesis System Instruction Manual. Li-Cor Ltd. Publication No. 8306-35, Revision 3, June 1985. 150p.

Manson, B.R., 1974. The life history of silver beech (*Nothofagus menziesii*). *Proceedings of the New Zealand Ecological Society*, **21**:27-31.

Matthews, M.A., Boyer, J.S., 1984. Acclimation of photosynthesis to low leaf water potentials. *Plant Physiology*, **74**:161-66.

Meinzer, F.C., 1982. Models of Steady-state and dynamic gas exchange responses to vapour pressure and light in Douglas fir (*Pseudotsuga menziesii*) saplings. *Oecologia (Berlin)*, **55**:403-408.

Mooney, H.A., Field, C., Williams, W.E., Berry, J.A., Bjorkman, O., 1983. Photosynthetic characteristics of plants of a Californian cool coastal environment. *Oecologia (Berlin)*, **57**:38-42.

Morris, J.Y., 1970. The evaluation of criteria for protection forestry. *New Zealand Journal of Forestry*, **15**:158-68.

New Zealand Forest Service, 1971. Utilisation of South Island beech forests. *Journal of the House of Representatives of New Zealand*, C 4 39p.

New Zealand Forest Service, 1980. Establishing Nursery-raised native trees. *What's new in Forest Research 86*. 4p.

New Zealand Meteorological Service, 1983. Summaries of climatological observations to 1980. New Zealand Meteorological Service Publication No. 177. 172p.

New Zealand Meteorological Service, 1984-86. Climatological Tables. Supplement to New Zealand Gazette. New Zealand Meteorological Service Publication No. 107.

New Zealand Soil Bureau, 1968. General survey of the soils of the South Island of New Zealand. New Zealand Soil Bureau, Department of Scientific and Industrial Research, Bulletin No. 27. 404p.

Nicholson, G., 1984. Methods of soil, plant and water analysis. New Zealand Forest Service, Forest Research Institute Bulletin No. 70.

Osonubi, O., Davies, W.J., 1980. The influence of plant water stress on stomatal control of gas exchange at different levels of atmospheric humidity. *Oecologia (Berlin)*, **46**:1-6.

Pearcy, R.W., 1983. The light environment and growth of C_3 and C_4 species in the understorey of a Hawaiian forest. *Oecologia (Berlin)*, **58**:19-25.

Pezeshki, S.R., Hinckley, T.M., 1982. The stomatal response of red alder and black cottonwood to changing water status. *Canadian Journal of Forest Research*, **12**:761-71.

Rawson, H.M., Begg, J.E., Woodward, R.G., 1977. The effect of atmospheric humidity on photosynthesis, transpiration and water use efficiency of leaves of several plant species. *Planta (Berlin)*, **134**:5-10.

Read, J., 1985. Photosynthetic and growth responses to different light regimes of the major canopy species of Tasmanian cool temperate rainforest. *Australian Journal of Ecology*, **10**:327-34.

Read, J., Hill, R.S., 1985. Photosynthetic responses to light of Australian and Chilean species of *Nothofagus* and their relevance to the rainforest dynamics. *New Phytologist*, **101**:731-42.

Reed, K.L., Hamerly, E.R., Dinger, B.E., Jarvis, P.G., 1976. An analytical model for field measurement of photosynthesis. *Journal of Applied Ecology*, **13**:925-42.

Rennison, G., 1963. Regeneration of the bush edge after fire in the Rangataua Forest. *Tane* **9**:91-96.

Schulze, E.-D., 1986. Carbon dioxide and water vapour exchange in response to drought in the atmosphere and in the soil. *Annual Review of Plant Physiology,* **37**:247–74.

Sakai, A., Wardle, P., 1978. Freezing resistance of New Zealand trees and shrubs. *New Zealand Journal of Ecology*, **1**:51-61.

Scholander, P.F., Hammel, H.T, Bradstreet, E.D., Hemmingsen, E.A., 1965. Sap pressure in vascular plants. *Science*, **148**:339-346.

Schulze, E.-D., 1970. Der CO_2-gaswechsel der Buche (*Fagus silvatica* L.) in abhangigkeit von den klimafaktoren im Freiland. *Flora (Berlin)*, **159**:177-232.

Schulze, E.-D., Hall, A.E., 1982. Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments. *in:* Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (eds.), Encyclopedia of Plant Physiology Volume 12B. Physiological Plant Ecology II. Water relations and Carbon Assimilation. Springer-Verlag, Berlin. p181-230.

Schulze, E.-D., Kuppers, M., 1979. Short-term and-long term effects of plant water deficits on stomatal response to humidity in *Corylus avellana* L. *Planta (Berlin)*, **146**:319-26.

Sharkey, T.D., Imai, K., Farquhar, G.D., Cowan, I.R., 1982. A direct confirmation of the standard method of estimating intercellular partial pressure of CO_2. *Plant Physiology*, **69**:657-9.

Smith, W.K., Hollinger, D.Y., 1987. Stomatal behaviour. *in:* Lassoie, J.P., Hinckley, T.M., (eds.), Techniques and Applications in Forest Tree Ecophysiology. CRC Press (in press).

Sokal, R.R., Rohlf, F.J., 1981. Biometry. 2nd edition, W.H. Freeman and Company, San Francisco, 859p.

Thornley, J.H.M., 1976. Mathematical models in plant physiology. A quantitative approach to problems in crop and plant physiology. Academic Press, London. 318p.

Thorpe, M.R., Warritt, B., Landsberg, J.J., 1980. Responses of apple leaf stomata: A model for single leaves and a whole tree. *Plant, Cell and Environment*, **3**:23-7.

Turton, S.M., 1982. Irradiance within montane tree canopies Craigieburn Range, New Zealand. M.Sc Thesis (Geography), University of Canterbury, New Zealand. 238p.

von Caemmerer, S., Farquhar, G.D., 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta (Berlin)*, **153**:376-87.

Wallace, L.L., Dunn, E.L., 1980. Comparative photosynthesis of three gap phase successional tree species. *Oecologia (Berlin)*, **45**:331-40.

Wardle, J., 1970. The ecology of *Nothofagus solandri*. 3. Regeneration. *New Zealand Journal of Botany*, **8**:571-608.

Wardle, J., 1983. An ecological basis for beech management in New Zealand. *New Zealand Journal of Forestry*, **28**:292-9.

Wardle, J., 1984. The New Zealand beeches. Ecology utilisation and management. New Zealand Forest Service. 447p.

Wardle, P., Campbell, A.D., 1976. Winter dormancy in seedlings of mountain beech (*Nothofagus solandri* var. *cliffortioides*) near timber line. *New Zealand Journal of Botany*, **14**:183-6.

Warrit, B., Landsberg, J.J., Thorpe, M.R., 1980. Responses of apple leaf stomata to environmental factors. *Plant, Cell and Environment*, **3**:13-22.

Webb, R.A., 1972. Use of the boundary line in the analysis of biological data. *Journal of Horticultural Science*, **47**:309-19.

Wilcox, M.D., Ledgard, N.J., 1983. Provenance variation in the New Zealand species of *Nothofagus*. *New Zealand Journal of Ecology*, **6**:19-31.

Wong, S.C., Cowan, I.R., Farquhar, G.D., 1979. Stomatal conductance correlates with photosynthetic capacity. *Nature*, **282**:424-6.

Woods, D.B., Turner, N.C., 1971. Stomatal response to changing light by four tree species of varying shade tolerance. *New Phytologist*, **70**:77-84.

Young, S.C., Whitehead, D., 1981. A Technique for the long-term measurement of irradiance on the forest floor. New Zealand Forest Service, Forest Research Institute, Tree Physiology report no. 36. (Unpublished). 7p.

ACKNOWLEDGEMENTS.

I wish to thank my supervisors James McWha, Ian McCracken and Dave Kelly for their interest and support during this project. Ian was an invaluable source of practical ideas, information and help and James was able to find finance to implement these ideas. Dave's involvement started when James left New Zealand for a more exciting position in Belfast. Their comments on the manuscript provided invaluable assistance in the production of the thesis.

I am grateful to the University Grant's committee for a Post Graduate Scholarship and to the Georgetti Scholarship Board for a Georgetti Scholarship. The U.G.C. also provided finance for the gas exchange system and pressure bomb. The Forest Research Institute of the New Zealand Forest Service financed the extensive travel and running expenses associated with this project, which would not have been possible without Forest Service support.

I would like to thank the large number of Forest Service personnel who have provided advice and assistance. I would particularly like to thank John Byers for his help with the construction of the lamps used at Station Creek. John Byers, Ian McCracken, Tony McSeveny and John Hunt were involved in building the access track for the generator at Station Creek. The generator and ancillary equipment were kindly loaned by the Forest Service. The nitrogen analyses were conducted by the revegetation laboratory at FRI Ilam. Tom Pearson produced the maps used in Figures 4.1 and 4.2.

I would like to thank Margaret Stevens for her help on the few occasions when I was in the Physiology Lab. My wife Jude has supported and tolerated me during the project and has assisted me with much of the field work, particularly the more unpleasant tasks.

Finally I would like to thank my two Robin friends at Station Creek who kept me company, feasted on my sandflies, and forgive them for trying to destroy the equipment.